

SCIENTIFIC AGRICULTURE

Vol. X.

MARCH, 1930

No. 7

THE EFFECT OF BREEDING IMMATURE EWES *

J. E. BOWSTEAD †‡

University of Alberta, Edmonton, Alta.

[Received for publication November 11, 1929]

INTRODUCTION

The preservation and development of size and reproductive ability are two essential factors for the successful maintenance of a herd, stud or flock. It has been frequently demonstrated and is almost universally believed that the future size and reproductive ability of the female stock can be seriously impaired or greatly improved according to whether or not intelligent selection is made of the parent stock used for each mating. Most of the improvement in size, thrift and breeding ability that has been secured in the development of our present day breeds of livestock has been the result of continued selection of the female as well as the male stock possessing a high standard of excellence.

Even though the development or even the preservation of the good qualities of a breed is dependent upon the intelligent selection of both dams and sires, such improvement or preservation of qualities is also dependent upon the breeding and feeding methods practiced. The feeding of unsuitable rations, the practice of inbreeding, and the breeding of immature animals are believed by most livestock men to temporarily or permanently decrease the size, thrift, and reproductive ability of either the dam or the progeny. Certain feeding experiments and inbreeding experiments have resulted in such decreases. But whether or not such decreases in size, thrift, or breeding ability is temporary or permanent, or in other words, whether such decreases are or are not inherited by the offspring, has not been definitely proved. Based upon our present idea of the permanency of genetic factors, if a reduction in size, thrift, and breeding ability is brought about by the feeding of unsuitable rations we would expect that normal size, thrift and breeding ability would be regained by the resumption of satisfactory feeding practices.

The results of inbreeding experiments are confusing because the decrease in size, thrift and breeding ability may be due to either lack of hybrid vigor, loss of size or reproduction factors or due indirectly to the presence or absence of other associated factors. Inbreeding may thus result in a temporary or permanent reduction in size, thrift or reproductive ability.

Experiments in which immature animals have been bred have confirmed the belief of the majority of livestock men that permanent reduction in size and thrift follows such a practice. Certain trials have indicated that immature males can be bred to mature females without apparently affecting the off-

*A thesis submitted to the Graduate School of the University of Wisconsin in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

†Associate Professor of Animal Husbandry.

‡The writer wishes to acknowledge the helpful criticism of Professors G. Bohstedt and L. J. Cole, under whose supervision this thesis was written.

spring. Such results seem logical when consideration is given to the fact that the male only contributes the sperm cell and takes no part in the development of the embryo.

The reciprocal mating of mature male and immature female is believed by most livestock men to cause serious consequences. Among the effects believed to result from such a breeding practice are:—

1. Reduction in size of dam as well as offspring.
2. Reduction in weight and vitality of offspring.
3. Increased mortality of dams and offspring due to increased difficulties at parturition and lower vitality of offspring.
4. Decrease in reproductive ability of both dam and offspring.
5. Accumulation of the effects if the mating of immature females is practiced through more than one generation.

From the present knowledge of growth and reproduction some of the above probable effects could be logically explained, while in other cases further research is necessary to secure a satisfactory explanation, as well as to find out whether such beliefs are well founded.

Although there is a need for further scientific knowledge of the effects of such a breeding practice from the standpoint of the biologist, there is also an urgent need for further knowledge of the effects from the standpoint of the breeder of farm livestock. Most successful breeders follow what could be called the "traditional" practice of breeding their mature or almost mature females. Improvement of the farm herd or flock has resulted from this method of breeding when intelligent selection and feeding has also been practiced. Even though the female young stock reach apparent sexual maturity before they become full grown, the general practice has been to delay their breeding until more growth has taken place. Such a breeding necessitates separating the immature from the mature females during the breeding season. This may not involve any additional equipment or labor under certain conditions and with certain classes of farm stock, but in the raising of cattle and sheep under range conditions and sheep or poultry under farm conditions the separation of immature from mature is not a small item as separate shelters, pastures or feed lots and feeding equipment must be provided. Extra labor is also involved.

To some farmers the effects of breeding immature females are not serious enough to warrant giving them separate attention. They have allowed their immature animals to run with the mature ones during the breeding season and have observed no ill effects. Some farmers have noted that often when an immature female has been accidentally bred the size and vitality of the offspring have been lowered. Considerable support is being given by some to the idea that if an immature female is so fed as to induce rapid growth she may reach a sufficient size to reproduce successfully at an early age. Why cannot those animals that appear to be sexually mature, but immature in size, breed and reproduce successfully without causing deleterious results? If wild animals breed successfully at puberty without causing a reduction in size and reproductive ability, why cannot immature domesticated livestock be also bred successfully?

The problem of whether or not to breed immature animals is an important one to sheep owners. Apparent sexual maturity is usually reached during the first breeding season when the ewe lambs are between six and nine months old. Under the usual practice of breeding, the ewe lambs are not bred until one year after they have reached sexual maturity. Success has followed this system of breeding. Some sheep owners have broken away from the usual custom because of either a lack of proof that immature breeding causes serious results, or because of neglect to make a separation of mature from immature animals. Others believe that, providing sufficient size has been obtained, success will follow the breeding of these ewe lambs.

There is confusion in the minds of many as to the effects and limitations of lamb-breeding, due mostly to lack of authentic information. If the size, thrift and reproductive ability of farm flocks will be reduced by following such a breeding practice, information should be secured to prove that yearling-breeding is the most profitable practice. If there is a commercial value in lamb-breeding to a limited extent, such limitations should be known.

The realization of this confusion of beliefs as to the effects and limitations of lamb-breeding, and of the lack of experimental proof to define such effects and limitations, prompted the Department of Animal Husbandry of the University of Alberta to initiate an experiment with sheep that would aid in the solution of this particular problem.

The following summary of published beliefs and experimental evidence relating to the breeding of immature animals is presented to show the inconsistency and inadequacy of the evidence.

STATUS OF THE PROBLEM

Authorities on the breeding and management of farm animals who have published text books on the subject are almost unanimous in the condemnation of the practice of breeding immature animals. Some of these men admit that experimental proof for their statements is lacking while others make no apparent effort to show upon what grounds their belief has been built.

On account of the fact that in 1878 much less was known of growth, reproduction and heredity than is now known, it is not surprising that Miles (1) did not question the belief that deleterious effects would follow the breeding of immature animals. "Predisposition to attacks of disease from slight exciting causes" and the increase in sterility and mortality rate of the progeny are mentioned as among the effects of immature breeding. He also quotes from an earlier book written by Dr. Duncan (2) in which is contained the statement of "two gentlemen skilled in the breeding of lambs and calves..... The mortality of the young of these animals when the mothers are immature is greater than when they are well grown..... I have no positive evidence to adduce in favor of this generally entertained notion" that premature breeding is "dangerous to the continued general health and prevents complete development of size and beauty." His own experience and the confirmation of his belief by many other authorities is given as a basis for his statements.

Davenport (3) in 1907, probably because of the scarcity of proof for deleterious effects of immature breeding, sets aside the subject with the following statement: "At what period the reproductive functions are most successful in producing young of a high order of excellence, whether in youth,

middle age or old age is not determined, though it is a point upon which light is badly needed. That there is danger in continued reproduction from immature animals, even though they are sexually vigorous, there is grave reason to fear; and yet, in general reproduction antedates maturity."

Mumford (4) in 1916 wrote that "the supposed evil results following premature pregnancy must be the result either of variations produced in the fundamental constitution of the germ plasm or in changes in the soma- or body-cells." If the effects of premature pregnancy are inherited by the offspring it "is contrary to our ideas of the inheritance of acquired characters." He suggests that a more accurate demonstration is needed to determine the nature of the effects of immature breeding.

In 1917 Potter (5) stated that "to breed ewes younger (than as yearlings) tends to diminish their size."

Marshall in his book on "The Physiology of Reproduction" (20) states that the practice of breeding of ewe lambs "is to be deprecated in the interests both of the ewes themselves and of their lambs".

Winters (6) in 1925 wrote that "the age at time of first breeding undoubtedly has an influence upon the female's fertility, but the degree has not been determined by experimental work. If breeding is delayed too long conception becomes more difficult and if the female is bred too early in life she seldom gains full maturity or her full inherent vigor, thus her life is shortened and her breeding powers are curtailed."

Rice (7) in his text book states in regard to "promiscuous early breeding" that "no good results and often poor or fatal ones may follow such careless management."

In 1927 Professor F. Kleinheinz (8) in his text book wrote that "lambs born from ewe lambs are generally small and weak and the mother too often is not supplied with enough milk for the young lamb. If the flock owner follows the practice of breeding ewe lambs, he will find in a few years that his flock is degenerating in size, constitution and weight of fleece."

Experiments have been conducted with classes of stock other than with sheep for the purpose of determining the effects of breeding immature females. Some experiments have been extensive enough to shed considerable light on the problem, while others have furnished fragmentary information. The results of all trials are not in agreement.

The experiment most similar to the trial being reported was one conducted by Mumford (9) who in 1908 began an experiment to determine "the effects of early mating upon the growth of immature females and their offspring." The results of his trials were as follows: Sows that were bred first at puberty but were liberally fed grew more slowly but reached a greater mature size and weight than later-bred sows. The average weight of the first pigs farrowed by the immature sows was only slightly less than those farrowed by the half-mature sows. More pigs were weaned by the immature sows than were weaned by the half-mature sows. Continuous immature breeding did not appear to cause a continued reduction in size if the average mature weight of the first ten generations is compared to that of the eleventh to sixteenth generation.

The effect of age of dam on offspring was noted by Stewart and Atwood (10) in their experiment to determine some "factors influencing the vigor of incubator chicks." Their series of experiments indicated that "the eggs from the young fowls (pullets) were smaller than the eggs from the older hens, and the chicks were smaller when they were hatched, grew more slowly, and more of them died from chick diseases than was the case with chicks hatched from eggs laid by mature mothers." Their experiments, however, did not show whether the mature weight of the chicks from pullet eggs was affected or whether there would be an accumulation of effects if the practice of incubating pullet eggs for the replenishing of the flock was continued.

Similar results were secured by Hays and Sanborn (11) in their experiments with poultry to find how the age of parent influenced the vigor of the offspring. Mature weights also were not considered and no effort was made to find out whether the mortality would increase in the second and third generation of pullet egg hatching.

Eckles (12 and 12a) in his study of growth and production records of dairy cows concluded that "from the standpoint of securing the greatest development as a dairy animal it is a decided disadvantage for a Jersey cow to calve under 24 months old, while nothing seems to be gained by allowing her to reach an age more than 30 months." He shows "that calving at an early age apparently does not admit the greatest development of the milking function." Eckles apparently did not take into account the effect of early breeding upon the offspring, which is one of the most important factors involved in the problem.

In a study of birth weight as an important factor in swine production Kuhlman (13) found that "while there is relatively little difference in the average birth weight of pigs from yearling sows and from those that are older there is a significant difference in the average weight of pigs from these two sources reaching 56 days and more of age. The results point clearly to the advantage in general of older sows over yearlings as mothers since they produce larger litters with less variability in size and they also take better care of their young. Many hog raisers make a practice of saving gilts almost entirely for breeding. By doing this they are missing the economic advantage to be gained from older sows."

Statistics on infant mortality (14) show that "babies of mothers under 20 and mothers 35 years or older showed higher mortality rates than other infants."

Ewart (15) in his study on the "influence of parental age on offspring" concludes that the reproductive life of a woman begins at puberty, increases rapidly till the 21st or 22nd year and more slowly till the 28th or 29th year. There is then a gradual decline with an abrupt fall to zero at the age of 38 or 39 years; and "in accordance with this age influence the physical and mental development and the vitality of the offspring varies."

It can be clearly seen that most of the experiments that have been conducted in the past have only yielded fragmentary information concerning the effects of breeding immature females. The results of these ex-

periments do, with the exception of the one by Mumford (9), indicate that size and thrift of dam and offspring are decreased by breeding immature females. Although reproductive ability of the offspring of the immatures-bred animal is one of the most important factors to be considered in the solution of this problem, little or no data have been reported in the foregoing trials.

The only difference between an animal bred early and one bred late is that the early-bred female experiences pregnancy and lactation at an early age. It is, therefore, important in studying the effects of breeding immature females, to know the effect that pregnancy and lactation have on growth and functional activity of females. The results of a few of the most outstanding experiments are mentioned in the following paragraphs.

The experiments of Minot (16), Baumm (17), Watson (18), Eckles (19) and Mumford (9) indicated that growth was not retarded by pregnancy. In some cases growth was enhanced. Marshall (20) in summarizing the changes during pregnancy states, "the maternal organism adapts itself to the progressively increasing requirements of the fetus, which dominates the metabolism of the mother. Under suitable dietary conditions this adaption is so successful that the maternal organism completes pregnancy with a gain."

The results of several experiments have shown that lactation retards growth. Eckles (12), using dairy heifers, found that "milk production is a severe tax upon the cow and checks the growth to a marked degree." By breeding the heifers early in life Eckles found that "if the retardation, especially in skeletal growth, has gone too far the animals will not, however, reach the normal size." The results of a Missouri experiment (21) with gilts indicated that "during lactation, growth is retarded and the stores of fats and minerals depleted." Mumford (9) found in his experiments with sows that during lactation growth is apparently inhibited, and Brody (22) in his growth studies states that "during lactation of these heavy-milking heifers there may be an actual loss, or at any rate decrease in growth, in body weight."

Reproduction has been shown by experiments to be influenced by feeding, breeding and age of mother. Not only have the functions of the generative organs been affected but the ability of the individuals to develop a fetus has been either increased or decreased. Evans, Bishop and Burr (23) have demonstrated the effect of plane of nutrition, kind of feeds, and specific vitamins, on the functioning of the reproductive organs before conception. Their work also extended to determining the effect of the same factors on the development of the fetus. At the Wisconsin Experiment Station it was found by Hart and his co-workers (24, 25, 26) that size and vitality of calves was influenced by the amount and kind of ration fed to the mother. The same results were found with pregnant ewes at the University of Alberta (27).

From the results of the experiments mentioned contradictory conclusions have been reached. Breeding immature females has caused a reduction in mature size of dairy heifers but the mature size of pigs was increased. A great mortality of offspring was secured when hatching pullet eggs as compared to hatching hen's eggs, but Mumford found that although the first litter of immature sows was less in number than the first litter of more

mature sows, a greater number of pigs was weaned by immaturesly-bred sows. Human infant statistics also indicate a higher mortality of babies from immature parents than from mature parents. The general belief that continued premature breeding would result in a decrease in size of breed is not substantiated by the results of Mumford with pigs.

The differences in the results of these trials are, no doubt, due to the differences in the class of animals used and the condition of the trials.

It is clearly seen that the previous trials have yielded results which in many cases are contradictory or have contributed only fragmentary information. With these facts in mind an experiment was planned from which could be secured results that related directly to the problem of the effects and limitations of lamb-breeding.

PLAN OF EXPERIMENT

The general plan followed in this experiment was the selection of two uniform groups of ewe lambs, one of which was bred as lambs and the other for the first time as yearlings. Both groups were bred in successive years until they had reached $3\frac{1}{2}$ years of age. The same ram was used on both groups of ewes each year and in no case was the breed of the ram changed during the time the ewes were in the experiment.

The progeny of ewes bred as lambs were also bred as lambs, and the progeny of the ewes bred for the first time as yearlings were likewise bred as yearlings. By so doing two strains of ewes resulted, differing only in the age at which they were first bred.

An effort was made to conduct the experiment under as near farm conditions as possible. Animals of all groups were maintained as one lot receiving the same feeds, care and shelter. The ewes were kept in a fair condition of flesh by receiving fair native, rape or cereal pasture in summer and oat, prairie, and alfalfa hays in about equal proportions in winter. No grain was fed the ewes except during a short period between lambing (late April and May) and the pasture period which commenced about June 8th. The lambs were not fed grain until after weaning when they were given similar grain mixtures for a short period till most of them had reached market weight (80 pounds).

Data were kept of the individual weights of all animals and a record was secured of their ability to reproduce. Detailed information was obtained on the weights and vitality of the lambs at birth, as well as their subsequent increase in weight and reproductive ability, until they reached the age of $3\frac{1}{2}$ years. Breeding, pre-lambing, and post-lambing weights were taken each year of all ewes. From the records kept, comparison could be made of the two systems of breeding. In other words, if the practice of breeding ewes for the first time as yearlings be regarded as a standard practice, then the results of this trial would show the effect of breeding ewe lambs. The effect of this breeding practice could be studied on the ewe lambs selected at the beginning of the trial as well as on the first and second generation produced by continued use of this breeding practice.

In order to eliminate the effect of season and to use a sufficient number of animals original ewe lambs were selected in 1921, 1922, 1923 and 1924. Four series of experiments were, therefore, conducted. Including the 98 original ewe lambs and their descendants, data have been kept on a total of 506 animals.

Animals failing either to come in season or failing to reproduce following mating were removed from the experiment in order that the data would only include records of ewes conforming to the breeding plan under which they had been placed. On the other hand, consideration of these animals is not ignored when failure to breed is believed to be an effect of the breeding practice used.

In any trial in which breeding stock is maintained on trial during a series of years, deaths, disease and accidents occur which necessitate their removal from the trial. A few individuals have been sold that should have been retained on trial, due to an error. These occurrences have reduced the number of animals in the respective groups.

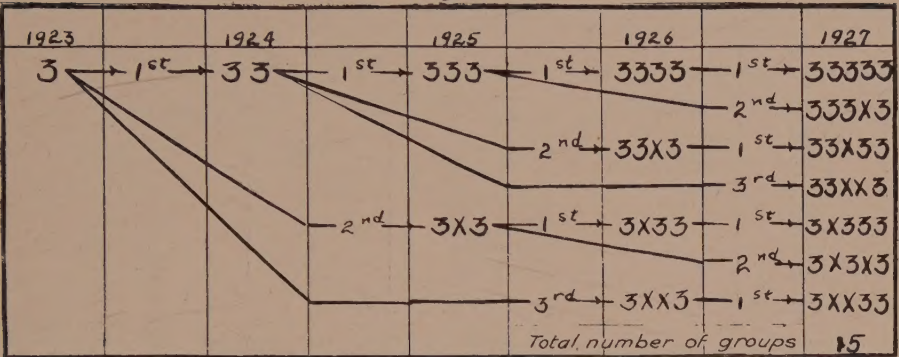
Under the systems of breeding practiced as previously outlined, the number of groups increased very rapidly. A system of nomenclature was devised which made the keeping of records more simple. The numerals 1, 2, 3 and 4 were used for the animals belonging to and resulting from the animals selected the first, second, third and fourth years. The letters O and X were used to represent a lapse of one year, O when the ewes were not bred and X when the ewes were bred.

Single numerals represent the lambs selected: 1 in 1927, 2 in 1922, 3 in 1923 and 4 in 1924.

The first lamb crops of these lambs are represented as 11, 22, 33 and 44 for the lambs dropped by ewes bred the first year, and 101, 202, 303 and 404 for the first lambs dropped by ewes not bred the first year. The second lamb crop from the selected ewes bred as lambs were classified as 1X1, 2X2, 3X3 and 4X4. It will be seen that by such figures, the breeding of animals is readily noted. 1XX1 represents the third lamb crop of the first group of selected lambs that were bred as lambs. 10X1 represents the second lamb crop of the first group of selected lambs that were not bred as lambs, but as yearlings. 3X3X3 would represent the second lamb crop from the second lamb crop dropped by the ewes selected in 1923 that were bred as lambs. 40404 would represent the first lamb crop from the first lamb crop of ewes selected in 1924, but were not bred as lambs, 20X2, 2XX2, 2X22 represent lambs dropped in 1925 and trace their origin to the lambs selected in 1922. 20X2 and 2XX2 are of the same breeding classification as 10X1 and 1XX1 except that the latter were dropped one year earlier. 2X22 represents the first lamb crop from the second lamb crop dropped by the ewes selected in 1922 that were bred as lambs.

The following diagram represents the number of groups resulting from any of the selected groups, but for convenience the groups resulting from the ewes selected in 1923 will be used.

CLASSIFICATION OF GROUPS RESULTING FROM
Lamb-breeding 1923 Ewes



Yearling - breeding 1923 Ewes

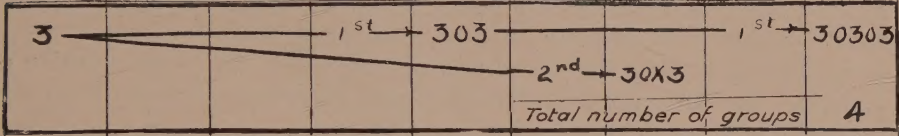


Chart I.

The above groupings indicate the increase in the number of possible groups resulting from the two groups of ewes selected in 1923. On account of the ewes being disposed of at 3½ years of age, 3XXX3 and 3OXX3 groups were not secured as they would represent the lamb crop of 4 year old ewes. In addition there was a natural decrease in the size of the groups, and individuals in some of the later classifications were not secured. When the lambs produced by one group of ewes is considered for one year, and the fact that about one-half of these were ram lambs, it will be seen that there would be a more or less gradual reduction in the size of the resulting groups.

RESULTS

EFFECT OF BREEDING EWE LAMBS FROM MOTHERS THAT WERE NOT BRED AS LAMBS.

As previously explained, a group of 28 lambs was selected in the fall of 1921. A Shropshire ram was placed with this group until 14 were believed to be safely in lamb. The two resulting groups (bred and unbred) were not as uniform in weight as they should have been, since as a general rule the more mature and heavier lambs were the ones that were bred.

To overcome this difficulty two uniform groups were selected in the fall of 1922, 1923 and 1924, one group in each year being bred. The fact that one or more of these did not come in heat, or failed to conceive, may have upset the uniformity of the two groups to a greater or less degree but the data secured from the two groups do not indicate that there was any decided lack of uniformity.

EFFECT ON MATURE WEIGHTS (3½ YEARS OF AGE)

The practice of breeding lambs apparently had no effect on the mature weight of the animals used. It will be seen from the following table that

two groups of bred lambs reached a greater weight than the corresponding unbred lambs, and the other two groups of bred lambs weighed less at $3\frac{1}{2}$ years of age than the corresponding unbred lambs.

TABLE 1. *Average weights at $3\frac{1}{2}$ years of age of lamb-bred ewes and yearling-bred ewes.*

Year of birth	Lamb-bred ewes		Yearling-bred ewes	
	Number of ewes	Average weight at $3\frac{1}{2}$ years	Number of ewes	Average weight at $3\frac{1}{2}$ years
1921	10	170.8 lbs.	14	173.1 lbs.
1922	10	170.2 lbs.	9	161.4 lbs.
1923	7	160.0 lbs.	13	166.8 lbs.
1924	7	166.0 lbs.	9	157.1 lbs.

The only factors which could have altered the relative difference in the mature weights of the two groups in any one year, in which two groups were selected would be difference in breeding of sire or dam and to a lesser extent, the differences in the number of twins represented in the two groups. Lack of uniformity in the groups used was not altogether due to the selection of animals. The chief factor was the removal of animals from the lot due to the failure to breed or death of animals selected.

When the average weights of the two groups were corrected for the factors mentioned above, which might have affected the results, the relative difference between the two groups was not altered.

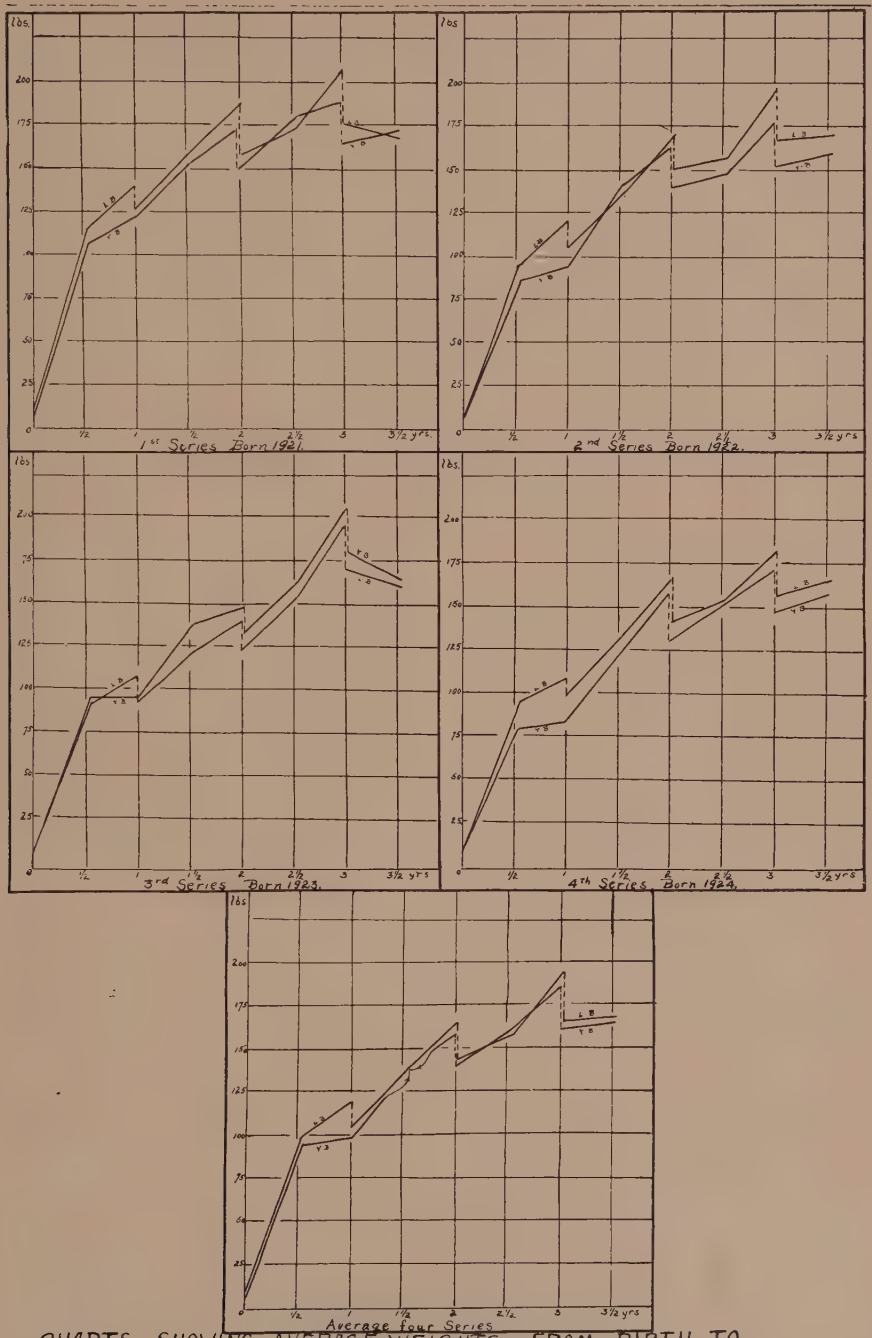
It may be reasonably assumed, therefore, that had the bred and unbred groups carried greater uniformity in the factors above mentioned, little or no change in the results would have been secured. In these trials the breeding of immature ewes was not followed by a decrease in their mature weights.

The average weight charts of each group from birth to maturity show that the rates of growth for the lamb-bred and yearling-bred groups were not the same. Differences in growth rate during any one season between these two groups were in most cases due to differences in pregnancy, lactation and average number of lambs they suckled.

Birth weights of these originally selected ewes were practically the same, the difference of only .53 pound being in favor of the lamb-bred group. At six months of age there was an average difference of 7.7 pounds in favor of the same group. This difference, however, has been previously explained as being due to the necessary removal of lambs from this group which failed to produce their first lamb crop.

Following the first six months period the lamb-bred ewes that were pregnant made more rapid gains than the yearling-bred ewes that were not pregnant. During the subsequent lactation period less rapid gains were produced by the lactating lamb-bred ewes than the yearling-bred ewes that were dry.

Based upon the weights of the four original lamb-bred and yearling-bred groups the average weights of both groups were equal at 18 months of age. It is apparent that the more rapid growth of the lamb-bred groups during their first six months and subsequent pregnancy was offset by the less rapid



CHARTS SHOWING AVERAGE WEIGHTS FROM BIRTH TO MATURITY OF ORIGINAL LAMB-BRED AND YEARLING-BRED EWES SELECTED IN 1921 - 1922 - 1923 - 1924.

Chart II.

growth during lactation, and following dry period previous to breeding at 18 months of age.

From 18 months to maturity the rates of growth were somewhat similar, differences only occurring when one or the other group of ewes were suckling a larger number of lambs.

Discussion

The results secured relative to the effect of breeding immature lambs on size are in accord with the finding of other investigators. Mumford (9) in his experiments with swine concluded that the difference in size and weight at maturity between animals bred at a very young age, and those bred at a later age was not significant. The immature-bred sows in his experiment reached maturity about twelve months after sows that were not bred until twenty-four months old. He also concluded that immature sows bred at five months and twice a year thereafter may be expected to develop into somewhat smaller animals at maturity than they would be if not bred until nearly mature. There was a retardation in the growth of sows due to lactation.

McKenzie (28) has summarized the latter work in Mumford's trial. His results differ from those reported by Mumford in that the "immature-bred sows reached a greater mature weight than the later bred sows. Certainly immature breeding did not inhibit growth. Whereas later-bred sows were fully grown at 35 to 45 months usually, early bred groups continued to grow till 80 to 90 months." This statement is based upon the mature weights of the original later-bred groups and their progeny and the mature weights of the first ten generations of early breeding. Although the data received from McKenzie were not complete the differences relative to time of maturity suggest that the time it took to reach maturity increased by the continued practice of breeding immature sows.

The increase in time required for immature-bred sows to reach maturity is probably due to the fact that they were bred twice yearly. The subsequent lactation periods retarded growth to such an extent as to delay maturity. In the Alberta experiment, however, the lamb-bred ewes apparently had sufficient time after their first lactation period to regain normal weight.

The results of these trials also suggest that the lamb-bred ewes by the time they reach sexual maturity are of sufficient size to reproduce and suckle their young without undergoing a retardation of growth. At the time the lamb-bred ewes were bred they had attained approximately 60 per cent of their mature weights. At 18 months of age both lamb-bred and yearling-bred ewes had reached about 84 per cent of their mature weights. Growth was apparently not retarded, neither did the results show an enhancement of growth as the report of McKenzie showed with pigs.

It has been mentioned that pregnancy apparently results in a more efficient utilization of feed nutrients and under liberal feeding may result in a gain in weight, and that during the subsequent lactation period growth may be seriously retarded. One would expect, therefore, that early breeding would not cause an increase in the animal's mature size or weight.

Retardation of growth whether by feeding sub-maintenance rations or lactation, is due to lack of available nutrients for growth. When a liberal ration is again fed or lactation is ended animals gain in weight at a faster rate than animals of the same age that have been on a liberal feed ration or that were not lactating. A severe or prolonged retardation of growth due to either cause has been found to result in a permanent stunting of the animals. The experiments conducted at the Missouri (29) and Kansas (30) Agricultural Experiment Stations with beef animals, as well as the experiment of Jackson and Stewart (31) with rats, indicate that permanent stunting may follow the feeding of sub-maintenance rations. Trials by Eckles with dairy heifers show that early lactation may cause a permanent retardation of growth.

Osborne and Mendel (32), however, found that normal mature weight will be attained if stunted animals are given a sufficient length of time. They state, "it appears as if the capacity to grow is only lost through exercise of this fundamental property of animal organisms."

Even though the results can be reasonably explained by stating that the lambs bred in these trials had attained sufficient size to experience pregnancy and lactation without lowering their mature weights or were allowed sufficient time to regain normal weight, another possible factor cannot be ignored. It is evident in table 2 that 24.5 per cent of the lambs selected for breeding failed to come in season or, following breeding, failed to produce a lamb. Those lambs failing to reproduce were removed from the experiment because they were of no further use. If their failure to breed was related to immaturity in size, the removal of those not reproducing would leave a group which could be regarded as having been more carefully selected for size than the yearling-bred group. The following classification of breeding weights indicates that between 70 and 100 pounds size was not a criterion for whether or not successful reproduction would occur.

Breeding Weights

Range in weight	Bred-lambs producing lambs	Bred-lambs failing to produce lambs
70— 80 pounds	3	1
80— 90 "	5	2
90—100 "	12	4
100—110 "	7	2
110—120 "	6	..
120—130 "	3	..

From the above figures it may be reasonably assumed that the elimination of some of the originally selected ewe lambs did not increase the chances for the lamb-bred group to reach the same weight as the yearling-bred group.

It may, therefore, be concluded that under the conditions of this trial ewe lambs, dropped by more mature mothers, can be bred as lambs without resulting in a decrease in their mature weight.

EFFECT UPON THE REPRODUCTIVE ABILITY OF ORIGINAL LAMB-BRED EWES

The comparison of the reproductive ability of the lamb-bred and yearling-bred ewe groups is of greater importance in the solution of the problem involved, than is a comparison of mature weights. Ewes bred as lambs produce one more lamb crop during their lifetime, but unless this extra lamb crop can be successfully and profitably raised, or unless the subsequent productive ability of the ewes is enhanced, the practice of breeding ewe lambs would not have any practical value.

Differences in the productive ability of animals is first evident in their ability to come in season and to develop a fetus. Since it was the practice in this experiment to hand-couple by either using a "teaser" to spot those in season, or to place a ram with the ewes for a short period each day, it was possible to keep accurate records of breeding dates of each ewe. The breeding period began in the early part of November and continued till the early part of February.

EFFECT ON ABILITY TO BE SUCCESSFULLY BRED

Failure to come in season or to develop a fetus was observed in each of the four lamb-bred groups. Animals unable to reproduce at any time during the trial were removed from the trial, since no further use could be made of these animals in the solution of the particular problem.

TABLE 2. *Showing unsuccessful mating of originally selected lamb-bred and yearling-bred ewes.*

Originally selected ewe lambs	At 7 to 8 months of age			At 19 to 20 months of age			At 31 to 32 months of age		
	Number in group	Number failing to come in season	Number bred but failing to produce lambs	Number in group	Number failing to come in season	Number bred but failing to produce lambs	Number in group	Number failing to come in season	Number bred but failing to produce lambs
1921 lamb-bred	15	*	3†	10	0	0	9	0	0
yearling-bred				15	0	1	10	0	0
1922 lamb-bred	12	0	2	10	0	0	9	0	0
yearling-bred				13	0	4	9	0	0
1923 lamb-bred	11	0	4	7	0	0	7	0	0
yearling-bred				13	0	0	13	0	0
1924 lamb-bred	11	2	1	7	0	0	7	0	0
yearling-bred				9	0	0	5	0	0

*On account of the fact that the first 15 lambs bred out of the 30 were used in this group, ewes failing to come in season were not noted.

†These ewes were allowed service during only one period of heat.

Table 2 shows the numbers of animals failing to come in season, and those failing to develop a fetus after being bred.

The reduction in number of ewes in any one group during successive gestation periods is due to the elimination of those not reproducing, deaths, and the fact that several were sold on account of chronic ailments or sold in error. There was, however, no significant difference in the number of deaths or ailments between the lamb-bred and yearling-bred groups.

It is evident from the above data that the originally selected lambs that were from mothers that were not bred as lambs, at six, seven and eight months of age usually come in season, only two lambs being noted that failed to accept the service of the ram. There was a tendency, however, for these lambs to fail to conceive or to lack the ability to develop a fetus. As no detailed examinations of the reproductive organs were made to determine whether actual fertilization of the ova had taken place, the specific reason for their failure to develop a fetus is not known. Out of the ten lambs that were bred, but failed to produce a lamb, nine produced lambs when bred the following year and one failed to produce a lamb. The five ewes bred for the first time as yearlings but failing to produce a lamb were sold and as a result no records were kept to determine their reproductive ability the following year.

The data show that only 75.5 per cent of the lambs selected for breeding produced a lamb while 90 per cent of the yearling-bred ewes were successfully bred. The reason for this failure to reproduce is not evident from the data kept, but it seems most logical to assume that it was due to undeveloped reproductive organs either failing to produce ova capable of being fertilized or failing to initiate the processes necessary for embryonic development.

The results seem to bear a relationship to other trials that have shown that fertility increases with age to maturity in size and decreases during senescence. The number of pigs in the litters of gilts are less than for more mature sows. Twinning is more frequent for mature ewes and cows than for young ewes and cows (33). The results would, therefore, indicate that the activity of the reproductive organs is probably related to the unsuccessful breeding of some of the ewe lambs.

It seems logical to assume that since fertility increases from zero to its maximum between puberty and maturity, females nearest puberty would show the greatest degree of sterility. The nearness to puberty would, therefore, be a greater factor influencing fertility than bodily weight or even the relationship between bodily weight at first breeding to mature weight.

EFFECT ON ABILITY TO PRODUCE A THRIFTY LAMB CROP

A comparison of the number, size, and vitality of the lambs dropped by the lamb-bred and yearling-bred groups of ewes is of great practical importance in the solution of this particular problem because it is an acknowledged fact that the profitableness of stock raising is greatly influenced by the number, size and thrift of the new born.

In comparing the reasons for weakness, stillbirths and deaths of the lambs dropped by both groups of ewes, no significant difference was apparent. In the yearling-bred groups, goitre was the cause of five weak lambs

TABLE 3. Showing the differences in the size and vitality of the lamb crops dropped by the four originally selected groups of lamb-bred and yearling-bred ewes.

Originally selected ewe lambs	At one year of age						At two years of age						At three years of age					
	Number of ewes	Per cent lamb crop	Per cent lamb crop weaned	Per cent of lambs born			Number of ewes	Per cent lamb crop	Per cent lamb crop weaned	Per cent of lambs born			Number of ewes	Per cent lamb crop	Per cent lamb crop weaned	Per cent of lambs born		
				Strong	Weak	Dead				Strong	Weak	Dead				Strong	Weak	Dead
1921 lamb-bred	12	108	54	62	31	7	10	120	92	83	17	—	9	211	95	95	5	0
yearling-bred	—	—	—	—	—	—	14	121	53	53	30	17	10	160	75	75	—	25
1922 lamb-bred	10	100	100	100	—	—	10	140	100	100	—	—	9	167	100	100	—	—
yearling-bred	—	—	—	—	—	—	9	156	100	100	—	—	9	156	100	100	—	—
1923 lamb-bred	7	100	57	71	29	—	7	129	89	89	—	11	7	171	100	100	—	—
yearling-bred	—	—	—	—	—	—	13	115	87	86	7	7	13	192	92	92	—	8
1924 lamb-bred	8	100	75	75	—	25	7	143	90	90	—	10	7	171	100	100	—	—
yearling-bred	—	—	—	—	—	—	9	144	100	100	—	—	5	160	88	88	12	—
Average lamb-bred	(37)	103	71	76	16	8	(34)	132	93	91	4	4	(32)	181	98	98	2	—
yearling-bred	—	—	—	—	—	—	(45)	131	83	83	10	7	(37)	170	89	89	2	9

and four stillbirths, while in the lamb-bred group goitre was the cause of three weak lambs and no stillbirths. No difficulty in lambing caused the death of lambs of the lamb-bred ewes, but three lambs died as the result of difficult lambing in the yearling-bred ewe groups. The reason for the remaining weak and stillborn lambs was not determined. No general tendencies toward any special ailment or abnormality throughout the life of the individuals or in any one year was noted such as respiratory, digestive disorders or disease of the udder.

Significant differences between the lamb crops of the two groups of ewes, were noted in the number of lambs born weak or dead as well as of lambs not reaching weaning age.

If the first lamb crops of the two groups are compared, the data show that the yearling-bred ewes produced considerably more lambs. The 1923 and 1924 ewes produced more thrifty lambs and the 1921 and 1922 groups produced lambs equal in thrift to those produced by the lamb-bred ewes of the corresponding groups.

Comparing the second lamb crops of both groups the data indicate that the yearling-bred ewes again produced a larger lamb crop than was produced by the lamb-bred ewes with no significant difference in thrift.

To summarize the comparisons of first and second lamb crops of the two groups it could be stated that the yearling-bred ewes have the greater reproductive ability due probably to their additional year's growth and development.

If, however, one compares the general thrift of the lamb crops dropped by both groups as two year olds and three year olds the lamb-bred ewes show a slightly greater ability to produce a thriftier lamb crop as indicated by the slightly greater number of lambs born and percentage of strong as well as weaned lambs. Such results would indicate that probably in the development of the first lamb crop an additional development of generative organs resulted that did not occur in the ewes that were open the first year.

Further evidence that the breeding of ewe lambs causes an additional increase in their ability to reproduce not obtained in ewes not bred till 18 months old was found in a study of the birth weights of the offspring of both groups of ewes.

It will be seen in table 4 that although the first lamb crop of the lamb-bred ewes are smaller than the first lamb crop of the yearling-bred ewes, the offspring of the lamb-bred ewes at two or three years of age were heavier. This would indicate that the ewes that had lambs at one year of age were able to develop heavier lambs in subsequent years than were ewes not bred as lambs.

While it is true that the first lamb crop of ewes bred as lambs was not satisfactory, it was not a total loss and under farm practice, some income would be earned from this lamb crop. Up to $3\frac{1}{2}$ years of age each ewe lamb that was bred produced a total of 3.74 marketable lambs, while the ewes not bred as lambs produced 2.60 marketable lambs.

TABLE 4. *Average birth weights of ram and ewe lambs dropped by the original lamb-bred and yearling-bred ewes.*

Four groups of originally selected ewes produced	At one year old				At two years old				At three years old			
	Number single off- spring	Average birth weight lbs.	Number twin off- spring	Average birth weight lbs.	Number single off- spring	Average birth weight lbs.	Number twin off- spring	Average birth weight lbs.	Number single off- spring	Average birth weight lbs.	Number twin off- spring	Average birth weight lbs.
Lamb-bred ewes Yearling-bred ewes	Ram lambs											
	15	8.7	2	7.6	11	12.2	15	9.5	6	12.2	20	10.3
	—	—	—	—	14	9.5	15	8.3	5	12.9	28	8.8
Lamb-bred ewes Yearling-bred ewes	Ewe lambs											
	21	8.2	—	—	12	9.8	7	9.1	2	11.5	29	9.8
	—	—	—	—	16	9.0	12	7.9	8	9.8	19	8.9

Discussion

The results obtained in this trial have opened up a field in which much work can be done. No work has apparently been done which would explain why the immature-bred lambs failed to develop a fetus. Several conditions may have been the cause, as (1) puberty may be followed by formation of atretic follicles which produce "heat" but no ova, (2) the conditions necessary for the sperm to remain or become active and capable of fertilizing the ova may not be suitable immediately following puberty, (3) death and resorption of embryo due to immature size uterus or lack of normal fetal nourishment. If any of these conditions was the cause of the bred lambs failing to reproduce, puberty cannot be regarded as a time when individuals are sexually mature.

Although it is known that pregnancy causes an increase in size of reproductive organs as well as mammary tissue, no experimental work is known to have been done relating to the effect of size of reproductive organs on number, size and thrift of offspring or amount of mammary tissue on gain in weight of young during the suckling period.

It seems logical to believe that the results secured in these trials are normal, the increased number of unsuccessful matings of the lamb-bred ewes being accounted for by a condition of the reproductive system or tract which is not favorable to reproduction and that the greater number, size and thrift of lamb crops at two and three years of age being due to a larger and more active reproductive system.

EFFECT OF BREEDING EWE LAMBS ON THEIR OFFSPRING

Even though lamb-breeding may result in an increase in total number of lambs produced in a ewe's lifetime or result in heavier lambs at birth, unless these lambs have the ability to grow and reproduce as successfully as the offspring of later-bred ewes the system of lamb-breeding should not be practiced.

EFFECT ON GROWTH

Ram lambs were castrated before ten days old and were sold when they had reached approximately 80 pounds. Most of these wether lambs reached market weight while still suckling mothers on pasture without grain being fed. Those not reaching market weight by about September first were weaned and grain fed till they weighed 80 pounds. The birth weights and average daily gain of the wether lambs dropped by the ewes belonging to the two different groups during the four years are shown in table 5.

In table 5 the average birth weights for the first lamb crops do not show the same relationship between the two groups as shown in table 4, where a more detailed analysis of birth weights was made, and as a result do not show that the lambs in the first lamb crop of the yearling-bred ewes were heavier than those of the lamb-bred ewes. As previously explained, as two and three year olds the lamb-bred ewes produced lambs that were decidedly heavier and somewhat stronger at birth than those dropped by the yearling-bred ewes at the same age. Studies made of the relationship between birth weight and subsequent gain by the writer with lambs and by Kuhlman (25) with pigs has shown that the heavier young make more rapid gains than the lighter ones.

TABLE 5. *Showing difference in average daily gain made by the male offspring of the originally selected ewes of both groups.*

Originally selected ewe lambs	At one year of age			At two years of age			At three years of age		
	Number of male off-spring	Average birth weight of off-spring	Average daily gain of off-spring	Number of male off-spring	Average birth weight of off-spring	Average daily gain of off-spring	Number of male off-spring	Average birth weight of off-spring	Average daily gain of off-spring
		lbs.	lbs.		lbs.	lbs.		lbs.	lbs.
1921 lamb-bred	1	9.1	.51	9	12.3	.58	6	10.9	.48
yearling-bred	—	—	—	5	8.2	.56	3	8.2	.48
1922 lamb-bred	6	9.1	.52	6	9.8	.56	5	10.5	.47
yearling-bred	—	—	—	2	8.4	.50	8	9.9	.48
1923 lamb-bred		None	lived	3	9.0	.50	5	11.9	.55
yearling-bred	—	—	—	5	8.5	.48	15	9.7	.48
1924 lamb-bred	—	One	unthrifty lamb	5	10.7	.49	4	11.2	.51
yearling-bred	—	—	—	7	10.4	.54	2	13.3	.56
Average four groups lamb-bred	7	9.1	.52	23	10.4	.53	20	11.1	.50
yearling-bred	—	—	—	19	8.9	.52	28	10.3	.50

There is sufficient reason to suppose that the lamb-bred ewes had a greater mammary development at two and three years of age than the yearling-bred ewes at the same age and, if so, one would expect that the wether lambs dropped by the lamb-bred ewes would show a significantly greater gain during the suckling period than the lambs from the yearling-bred ewes. This significant difference in gain is not brought out in table 5, which indicates that with the advantage of a greater birth weight and strength and a better milking mother, the lambs of the lamb-bred ewes were unable to make more rapid gains. Slightly more rapid gains were made in most years but less rapid gains were also made in a number of cases. These results would lead one to the conclusion that there was a possibility that the lambs from the lamb-bred mothers were unable to make gains as efficiently as did the lambs from the yearling-bred mothers. It may be stated, however, that lamb-breeding did not cause a reduction in the rate of gains made by the offspring during the suckling period.

The above figures, however, only include the rate of gains of the wether lambs, during their suckling period. The difference in subsequent growth following the suckling period up to maturity is shown by comparing the weights of the ewe lambs dropped by the two different groups of ewes with the mature weights of their dams. The ewe lambs were handled in the same way through the suckling and weaning period.

The scarcity of numbers of individuals represented in table 6 is due to the fact that in many cases the dams or daughters were removed from the trials by failure to reproduce, death or chronic ailments which made them unsuitable for further use in the trial. Only daughters reaching maturity whose dams likewise reached maturity are shown in table 6.

Based upon group as well as individual averages the ewe lambs from the lamb-bred ewes did not grow to the same relative mature weight as the ewe lambs from the yearling-bred ewes. The daughters of the lamb-bred ewes weighed at maturity an average of 14.3 pounds less than their dams, while the daughters of the yearling-bred ewes weighed .3 pounds less than their dams. Twenty-two out of thirty-four daughters of the lamb-bred ewes showed a mature weight which was greater than .3 pounds below the mature weight of their dams and sixteen out of twenty-four daughters of the yearling-bred ewes showed a greater mature average weight than 14.3 pounds less than their dams. In other words, the relative weights of thirty-eight out of fifty-eight daughters of ewes in both groups indicated that lamb-breeding tended to retard the mature weight of the daughters.

Even if the results had been more significant they would not have necessarily been in disagreement with the gains made by the wether lambs, since conditions for growth during the suckling period are somewhat different to the conditions for growth in later life.

Mention has been made of the fact that there is a relationship between birthweight and subsequent growth as was found by the writer in a study of lamb weights and Kuhlman in a study of pig weights. This could be used to account for the good growth made during the suckling period by the wether lambs dropped by the lamb-bred ewes. No results of other experimental work can be submitted to account for the decrease in weight of the daughters. Most authorities in text books claim that such results are liable to occur but give no experimental proof for their statements.

Discussion

The results do not show conclusive evidence that reduction in rate of gain during the suckling period or that a decrease in mature weight of offspring follows lamb-breeding. Certainly no reduction in rate of gain was found with wethers during the suckling period. Insufficient number of mature weights were secured to make conclusions regarding the effect of immature breeding on mature size. The tendency appeared to be to a reduction in size. As will be discussed later, the reproductive ability of the same offspring seemed to be associated with age because improvement was secured as the lamb-bred mothers became older. If there is a relationship between age and reproductive ability one would expect that the first crop of lambs from lamb-bred mothers would show the greatest decrease in mature weight, the second crop of lambs from same mothers larger mature weight, and the third lamb crop normal mature weight or equal to that of the lambs dropped by the three year old yearling-bred ewes.

It seems logical to believe that when lamb-bred mothers reach mature size they should be able to produce a normally growing and reproducing lamb crop.

TABLE 6. *Showing differences between the mature weights of the original selected ewes of both groups and their daughters.*

Originally Selected Ewes	When one year old						When two years old						When three years old					
	Number of Daughters	Av. mature weight of daughters	Av. mature weight of dams	Difference in favor of daughters	lbs.	lbs.	Number of Daughters	Av. mature weight of daughters	Av. mature weight of dams	Difference in favor of daughters	lbs.	lbs.	Number of Daughters	Av. mature weight of daughters	Av. mature weight of dams	Difference in favor of daughters	lbs.	lbs.
1921	1	147.1	170.0	-22.9	—	—	2	181.3	178.0	—	—	—	5	161.1	173.4	-12.3	—	—
Lamb-bred	—	—	—	—	—	—	—	—	—	—	—	—	2	179.4	175.6	3.8	16.1	—
Yearling-bred																		
1922	1	162.0	172.0	-10.0	—	—	3	157.7	178.7	-21.0	—	—	8	155.7	176.0	-20.3	—	—
Lamb-bred	—	—	—	—	—	—	4	140.6	152.1	-11.5	9.5	—	6	162.6	156.3	6.3	26.6	—
Yearling-bred																		
1923	—	—	—	—	—	—	3	148.2	161.1	-12.9	—	—	4	170.8	162.1	8.7	—	—
Lamb-bred	—	—	—	—	—	—	4	192.1	180.8	11.3	24.2	—	3	168.3	168.0	.3	-8.4	—
Yearling-bred																		
1924	—	—	—	—	—	—	2	171.0	186.6	-15.6	—	—	7	*153.4	*170.1	-16.7	—	—
Lamb-bred	—	—	—	—	—	—	—	—	—	—	—	—	3	*127.7	*148.7	-21.0	-4.3	—
Yearling-bred																		

*2½ year old weights.

EFFECT ON REPRODUCTIVE ABILITY

A decrease in the ability to reproduce was noted in the lambs dropped by the lamb-bred ewes as compared to the daughters of the yearling-bred ewes. This can be shown by comparing the percentages of successful matings as well as the vitality of the lamb crops at birth and percentage of the lamb crop weaned for the two groups.

TABLE 7. *Showing reduction in number and percentage successful matings by breeding ewe lambs.*

Lamb crop of ewes	At one year of age				At two years of age				At three years of age			
	Number of ewes	Number failing to come in season	Number bred but failing to produce lambs	Percentage successful matings	Number of ewes	Number failing to come in season	Number bred but failing to produce lambs	Percentage successful matings	Number of ewes	Number failing to come in season	Number bred but failing to produce lambs	Percentage successful matings
<i>Dams</i>												
4 original groups of lamb-bred ewes	49	2	10	75.5	34	0	0	100	32	0	0	100
4 original groups of yearling-bred ewes					49	0	4	92	37	0	0	100
<i>Daughters</i>												
1st lamb crop of above lamb-bred ewes	12	4	4	33.3	3	0	0	100	2	0	0	100
2nd lamb crop of above lamb-bred ewes	14	4	1	64.3	8	0	0	100	7	0	0	100
3rd lamb crop of above lamb-bred ewes	7	0	2	71.4	5	0	0	100	5	0	0	100
1st lamb crop of above yearling-bred ewes					11	0	0	100	11	0	0	100
2nd lamb crop of above yearling-bred ewes					18	0	2	89	12	0	0	100

Table 7 shows that in this trial the practice of breeding ewe lambs through only one generation resulted in a decrease in successful matings from 75.5 per cent to 33.3 per cent for the first lamb crop of the lamb-bred mothers. Additional maturity of the lamb-bred mothers tended to improve the fertility of their second and third lamb crops to 64.3 per cent and 71.4 per cent respectively. The data for both dams and daughters of the lamb-bred groups at two and three years of age showed no unsuccessful matings because all ewes failing to breed successfully as lambs were necessarily removed from the experiment.

A study of individual breeding weights of lamb-bred dams and daughters was made to find out whether the failure of the daughters to breed was due to their being less mature than their mothers. The daughters in the first, second and third lamb crops were found to weigh less at first breeding time than their dams weighed at their first breeding time, the average difference being 16.8 pounds, 8.0 pounds and 11.5 pounds respectively. The daughters in

the first and second lamb crops of the yearling-bred ewes weighed an average of 10.2 pounds and 6.6 pounds less than their mothers at seven or eight months of age. The fact that the first daughters of the lamb-bred ewes weighed 16.8 pounds less at first breeding time may have accounted for some of the unsuccessful matings of the daughters. Had the weights of the unsuccessfully mated lambs been taken at seven to eight months of age definite proof might have been secured, had their weights been less than 70 pounds.

The practice of breeding ewes for the first time as yearlings did not reduce the breeding ability of their offspring. Ninety-two per cent successful matings for 49 dams compares favorably to 100 per cent and 89 per cent successful matings for their first and second lamb crops respectively. None of the dams or offspring failed to come in season when first bred as yearlings which is in contrast to the results for lamb-bred dams and daughters.

The results indicate, therefore, that the practice of breeding ewe lambs tended to increase the number of unsuccessful matings in offspring.

Comparing the ability of offspring of the originally selected ewes of both groups to produce a thrifty lamb crop indicates that the practice of lamb-breeding lowers the reproductive ability of the offspring as shown in table 8.

Although the number of ewes represented in some of the groups is small, the data indicate that the ability to produce a thrifty lamb crop is decreased by the practice of lamb breeding. The decrease may be noted in the percentage of the lamb crops surviving the first few months of life, the mortality rate being greatest for the first lamb crop dropped by the first daughters of the original lamb-bred ewes. The data on the groups of daughters from the lamb-bred ewes, indicate a tendency for the percentage of lamb crop weaned to be related to the maturity or age of the dam and grand-dam, or in other words to the amount of immaturity of both dam and grand-dam. Of the first lamb crop from ewes that were themselves the first lamb crop of lamb-bred ewes only 50 per cent were weaned. Of the second lamb crop from the same ewes 80 per cent were weaned. The following condensed chart shows more clearly the effect of ewe lamb-breeding.

PERCENTAGE OF LAMB CROPS WEANED

		AGE OF DAM		
		1	2	3
Age of	1	50	80	100
grand-dam	2	62	100	100
	3	100	60*	100

*No reason can be given for this relatively poor lamb crop since their dams when one year of age dropped a 100 per cent thrifty lamb crop.

The results of this trial indicate that the thriftier lamb crop is secured from mature daughters of mature ewes, and a less thrifty lamb crop from immature daughters of immature ewes or, in other words, by practicing lamb-breeding.

TABLE 8. Showing decrease in vitality of lamb crop through the practice of breeding ewe lambs.

Lamb crop of ewes	At one year of age						At two years of age						At three years of age					
	Number of ewes	Per cent lamb crop	Per cent lamb crop weaned	Per cent of lambs born			Number of ewes	Per cent lamb crop	Per cent lamb crop weaned	Per cent of lambs born			Number of ewes	Per cent lamb crop	Per cent lamb crop weaned	Per cent of lambs born		
				Strong	Weak	Dead				Strong	Weak	Dead				Strong	Weak	Dead
<i>Dams</i>																		
4 original groups of lamb-bred ewes	37	103	71	76	16	8	34	132	93	91	4	4	32	181	98	98	2	0
4 original groups of yearling-bred ewes	—	—	—	—	—	—	45	131	83	83	10	7	37	170	89	89	2	9
<i>Daughters</i>																		
1st lamb crop of above lamb-bred ewes	4	100	50	75	—	25	3	167	80	100	—	—	2	150	100	100	—	—
2nd lamb crop of above lamb-bred ewes	8	100	62	75	12½	12½	8	162	100	100	—	—	7	171	100	100	—	—
3rd lamb crop of above lamb bred ewes	6	100	100	100	—	—	6	167	60	60	30	10	5	140	100	100	—	—
1st lamb crop of above yearling-bred ewes	—	—	—	—	—	—	11	145	100	100	—	—	8	200	75	81	19	—
2nd lamb crop of above yearling-bred ewes	—	—	—	—	—	—	16	156	84	84	16	—	12	175	90	90	5	5

Discussion

The preceding data, relative to the effect of lamb-breeding on the growth and reproductive ability of the offspring, have indicated that although the growth of the originally selected ewes was not affected, 38 out of 58 of their offspring failed to reach relatively as high a mature weight as the offspring of the yearling-bred ewes. As has been pointed out, this difference was not significant, due to the variability in the mature weights of the offspring. Had it been possible to control the date of lambing, size of lamb crop, length of time and number of lambs that suckled each ewe, the writer believes that the results might have shown that a reduction in size would only be obtained in offspring of immature mothers. If such results were secured they would be contradictory to those secured by McKenzie (28) with pigs, but would be in partial agreement with the general belief based upon the experiences of livestock men. It seems logical that a relationship should exist between size and reproductive ability, because one would expect sexually vigorous animals to reach a greater size than those not so vigorous.

Reproductive ability of the offspring at seven to eight months of age was reduced by lamb-breeding, being especially true when the offspring were dropped by one year old mothers. The maintenance of normal reproductive ability of the originally selected lamb-bred ewes seems logical since development was not retarded beyond 18 months. The fact that the first offspring of the lamb-bred ewes were about 17 pounds lighter at seven to eight months of age than their mothers probably accounts for their inability to successfully breed and produce a thrifty lamb crop. Lack of development in size is also accompanied by lack of development and activity of the sex organs, as found by Evans and Bishop (23) when growth was retarded by feeding sub-maintenance rations.

Prior to and following puberty there is not only a growth in size and activity of the reproductive organs, but there is a change in size and activity of the endocrinous glands known to be associated with sexual development. Puberty involves a period of reorganization. If pregnancy occurs before the reorganization is complete it seems logical to suppose that the offspring may be profoundly affected not only in size but in reproductive ability. Sexual precocity may be the result of domestication but it is not necessary to believe that the period of successful reproduction is lengthened, or that the offspring of immature parents need be as large or as vigorous as their mothers.

EFFECT OF BREEDING EWE LAMBS THROUGH MORE THAN ONE GENERATION

In the previous section the results and discussion were confined chiefly to the originally selected ewe lambs and their offspring. Although the results indicated that reproductive ability and probably size were affected, more conclusive evidence regarding the effect of lamb-breeding as contrasted with the usual practice should be secured by continuing lamb-breeding through more than one generation.

It was not realized at the beginning of the trial that the number of individuals making up the first, second and third generations would decrease as rapidly as occurred in this trial. Starting with 49 ewe lambs to be bred as lambs no females were produced in the third generation that reproduced successfully. Table 9 shows how rapidly the number of individuals declined from one generation to the next.

TABLE 9. *Showing number and disposition of individuals in the first, second and third generations of lamb-breeding and yearling-breeding.*

Original selected ewe lambs	Number lambs	Number males	Number females	Percent deaths of females	Per cent unsuc- cessful matings	Per cent females sold in error	Balance left to produce next generation	
							Number	Per cent
lamb-bred yearling-bred	—	—	49	—	24.5	—	37	75.5
	—	—	50	—	10.0	—	45	90.0
1st generation lamb-breeding yearling-breeding	38	17	21	43	38	—	4	19
	58	28	30	37	—	23	12	40
2nd generation lamb-breeding yearling-breeding	4	2	2	—	—	—	2	100.0
	16	9	7	29	14*	—	4	57
3rd generation lamb-breeding yearling-breeding	2	—	2	50	50	—	—	—
	5	3	2	50	—	—	1	50

*Irregularity in the recording of data made the breeding record of this individual doubtful.

The reduction in the number of individuals in the first, second and third generations of lamb-breeding was due to the small lamb crop, deaths and unsuccessful matings. In the first, second and third generations of yearling-breeding the reduction in number was due to deaths and the fact that seven females of the first generation were sold. At the time some of these were sold, it was thought that it was only necessary to retain a fair number of ewes to represent the first generation so that whenever twin ewe lambs were dropped one was sold and the other retained. The data, however, clearly indicate that there was a more rapid reduction in numbers of individuals in the first, second and third generations of lamb-breeding due to unavoidable causes, than was the case of yearling-breeding.

EFFECT ON GROWTH

Small numbers of individuals in the latter generations made impossible a direct study of the effect of growth and reproductive ability. When the mature weights of the females through the generations was attempted too many individuals were necessarily removed from the trial before they had reached $3\frac{1}{2}$ years of age. It was necessary merely to group the individuals in each generation and use their average weights. The average weights for two generations are shown in table 10.

TABLE 10. *Showing average weights of individuals in first and second generation of lamb-breeding and yearling-breeding.*

	Number of individuals	At 3½ years of age
4 originally selected groups of lamb-bred ewes	34	166.7 lbs.
1st generation (1st offspring of above ewes)	3	158.2 lbs.
2nd generation (1st offspring of above 1st generation)	2	162.5 lbs.
4 originally selected groups of yearling-bred ewes	45	164.6 lbs.
1st generation (1st offspring of above ewes)	5	153.5 lbs.
2nd generation (1st offspring of above 1st generation)	5	154.9 lbs.

It will be noted in the above table that the first and second generations of both lamb-breeding and yearling-breeding weighed less than the original ewes. This was no doubt due to the fact that the original ewes were bred to a Shropshire ram.

The data obtained in this trial do not indicate a tendency for a reduction in size of the first or second generation due to lamb-breeding. It will be noted in the above table that the average mature weights of the first and second generations of lamb-breeding were slightly higher than the average mature weights of the first and second generations of yearling-breeding. Due to the small number of individuals represented in the first and second generations the results could not be regarded as significant.

EFFECT ON REPRODUCTIVE ABILITY

The effect of lamb-breeding through one generation has been already considered (see page 447). Since only four females were secured in the second and two in the third generation, there would be little value in presenting the data on their reproductive ability for comparison with that of the yearling-bred groups. Fairly conclusive results were secured to show that the first generation of lamb-breeding resulted in a decrease in successful matings and vitality of offspring sufficient to condemn the use of lamb-breeding for the production of females to replenish the flock.

Discussion

An insufficient number of animals was available to determine satisfactorily the effect of lamb-breeding through a series of generations. The rapid decrease in numbers of individuals representing the first, second and third generations indicates that a much greater number of originally selected ewes than used in this trial is necessary in order to secure sufficient individuals for the second and third generations. The rapid decrease also indicates that the percentage of lambs in any flock, that were dropped by immature dams, and capable of being bred is small.

Sufficient evidence has been presented to show the effect of lamb-breeding on the offspring and to prove the inadvisability of using this system of breeding for the production of ewe lambs to replenish the flock.

SUMMARY

Effect of lamb-breeding on the originally selected ewe lambs:

1. Lamb-breeding did not cause a decrease in mature weight. Ewe lambs of both lamb-bred and yearling-bred groups reached about the same mature weight.
2. More ewes bred as lambs failed to produce offspring than did ewes bred as yearlings. The number of unsuccessful matings was greater with lambs than with yearlings.
3. The first crop of lambs from the lamb-bred ewes was lower in number and vitality than the first lamb crop of the yearling-bred ewes.
4. The lamb-bred ewes at two and three years of age produced more lambs, heavier and thriftier lambs than the yearling-bred ewes produced at the same ages.
5. More marketable lambs were produced in the first three lamb crops of the lamb-bred ewes than were produced in the first two lamb crops of the yearling-bred ewes.

Effect of lamb-breeding on offspring:

6. Wether lambs from lamb-bred mothers made as good gains during the suckling period as wether lambs from yearling-bred mothers.
7. Most of the ewe lambs from lamb-bred mothers did not reach the same mature weight as ewe lambs from yearling-bred mothers, where comparison was based upon the mature weights of their dams. The significance of the results may be questioned due to extent of variability.
8. The first ewe lambs from lamb-bred ewes were less able than their mothers to come in season or to conceive.
9. The first ewe lambs from lamb-bred mothers produced a less thrifty lamb crop than did their mothers.
10. The second and third crop of ewe lambs from lamb-bred mothers were more successfully bred and produced a more thrifty lamb crop than did the first crop of ewe lambs from the same mothers.

Effect of lamb-breeding on offspring through several generations:

11. Lamb-breeding caused such a rapid reduction in the number of individuals representing the second and third generation that significant results could not be secured. A much greater number of ewe lambs than selected at the beginning of this trial would be necessary to determine the effect of continued lamb-breeding.
12. That there would be a reduction in mature weight or reproductive ability by continuing lamb-breeding through several generations could not be established due to the rapidly diminishing numbers.

CONCLUSIONS

The data indicate that the problems arising out of the breeding of ewe lambs are in actual practice of less importance than they may appear. Lamb-breeding results in a decrease in the percentage of successful matings as well as a decrease in the percentage of lambs raised to weaning age. The numbers

of ewes representing the second, third, or later generations would be rapidly reduced so that in any flock there would be only a relatively small proportion of these lambs.

The first lambs of lamb-bred mothers are not as large, nor as thrifty and do not possess the breeding ability of lambs produced in subsequent years. This first lamb crop, however, may be considered an extra lamb crop, if comparison is made to the standard practice of breeding yearlings, and this crop, therefore, yields an additional income.

The most important finding in favor of lamb-breeding is that the original lamb-bred ewes at two and three years of age produce a greater number of lambs, also heavier and stronger lambs than yearling-bred ewes of the same age. The results indicate that this improvement in reproduction may be secured under farm conditions by following a system of lamb-breeding limited to ewe lambs from mature mothers. Under this system it is evident that all lambs from immature mothers should be sold, because such lambs will not reproduce as satisfactorily as lambs from mature mothers. Even though, as was demonstrated in these trials, only about 75 per cent of ewe lambs from mature dams could be successfully bred, the total production, size and thrift of the lamb crop at birth would be increased and the ultimate size of the ewes composing the flock would be maintained under a system of lamb-breeding limited to ewes from mature mothers.

LITERATURE CITED

1. MILES. Stock Breeding. p. 36. 1878.
2. DUNCAN. Fecundity, Fertility and Sterility. p. 38.
3. DAVENPORT. Principles of Breeding. p. 95. 1907.
4. MUMFORD, F. B. The Breeding of Animals. p. 272. 1916.
5. POTTER. Western Live Stock Management. p. 179. 1917.
6. WINTERS, L. M. Animal Breeding. p. 238. 1925.
7. RICE. Breeding and Improvement of Farm Animals. p. 53. 1926.
8. KLEINHEINZ. Sheep Management, Breeds, and Judging. p. 18, 1927.
9. MUMFORD, F. B. The effect on growth of breeding immature animals. Mo. Agric. Exp. Sta. Res. Bul. 45. 1921.
10. STEWART and ATWOOD. Some factors influencing the vigor of incubator chicks. W. Va. Agric. Exp. Sta. Bul. 124. 1909.
11. HAYS and SANBORN. Vigor in production-bred flocks. Mass. Agric. Exp. Sta. Bul. 242. 1928.
12. ECKLES, C. H. The ration and age of calving as factors influencing the growth and dairy qualities of cows. Mo. Agric. Exp. Sta. Bul. 135. 1915.
- 12a. ——— and SWETT, W. W. Some factors influencing the rate of growth and the size of dairy heifers at maturity. Mo. Agric. Exp. Sta. Bul. 31. 1918.
13. What's new in farm science. Wis. Agric. Exp. Sta. Bul. 405. 1929.
14. U. S. D. Labor. Infant mortality and its causes. Science N.S. 58: 1497. 1923.
15. EVART, R. J. Influence of parental age on offspring. Eugenics Review 3: p. 201.
16. MINOT, C. S. Semescence and rejuvenation. Jour. of Physiol. 12: p. 97. 1891.
17. BAUMM. Gewichtsveränderungen der Schwangen etc. Inaug. - Dessert., Michen 1887.
18. WATSON, J. B. The effects of the bearing of young upon the body weight of the female white rat. Jour. Comparative Neurology. 15: 6, p. 514. 1905.
19. ECKLES, C. H. The nutrients required to develop the bovine fetus. Mo. Agric. Exp. Sta. Res. Bul. 26. 1916.
20. MARSHALL, F. H. A. The Physiology of Reproduction. 1922.

21. GRISWOLD, TROWBRIDGE, HOGAN, HAIGH. The effect of gestation and lactation upon the growth and composition of swine. Mo. Agric. Exp. Sta. Res. Bul. 114. 1928.
22. BRODY. Growth and development. 8: Mo. Agric. Exp. Sta. Res. Bul. 103. 1927.
23. EVANS and BURR. The antisterility vitamine, fat soluble E. Memoir Univ. of California. 8: 1928.
24. HART, STEENBOCK and HUMPHREY. New facts for successful growth and reproduction. Wis. Agric. Exp. Sta. Bul. 287. 1918.
25. RUSSELL and MORRISON. New farm facts. Wis. Agric. Exp. Sta. Bul. 323. 1920.
26. HART, STEENBOCK and HUMPHREY. Influence of rations restricted to the oat plant on reproduction in cattle. Wis. Agric. Exp. Sta. Res. Bul. 49. 1920.
27. DOWELL and BOWSTEAD. Rations for breeding ewes. University of Alberta. Bul. 1. 1922.
28. McKENZIE, F. F. Information to author. 1929.
29. TROWBRIDGE, MOULTON and HAIGH. Changes in form and weight on different planes of nutrition. Mo. Agric. Exp. Sta. Res. Bul. 43. 1921.
30. WALTERS, COCHEL and VESTAL. Kansas Industrialist, May 10, 1913. April 18, 1914.
31. JACKSON and STEWART. Ultimate effects of inanition in size. Jour. Exp. Zool. 30: 1, p. 97. 1920.
32. OSBORNE and MENDEL. The suppression of growth and the capacity to grow. Jour. B.C. 18: p. 95, 1914. 23: p. 439. 1915.
33. JONES and ROUSE. Multiple births in cattle and sheep. Jour. Dairy Science. 3: 4, p. 260. 1920.

INHERITANCE IN BARLEY WITH SPECIAL REFERENCE TO THE COLOR OF CARYOPSIS AND LEMMA.*

G. F. H. BUCKLEY†

Dominion Experimental Farm, Brandon, Man.

INTRODUCTION

The great number of cultivated varieties and strains, each differing from the other in one or more heritable variations, makes barley exceptionally valuable for genetical study. The chromosome number ($n=7$) is comparatively small, and consequently a correspondingly small number of linkage groups is possible.

Although there is a vast amount of literature dealing with inheritance in barley, knowledge of the subject is still very limited. The inheritance of relatively few characters is known. Linkage relations and the establishment of linkage groups have been attempted in a few cases. Color of caryopsis and lemma is used considerably in the classification of barley varieties, yet the inheritance of color has received comparatively little study. The purpose of the present investigation is to add to the knowledge of inheritance in barley, particularly with respect to color in the caryopsis and lemma, and by a study of the interrelations between genes to establish linkage groups.

REVIEW OF LITERATURE

In this review only those papers which are directly concerned with the present study will be discussed.

INHERITANCE OF COLOR

The majority of reports concerning the inheritance of color in barley deal only with color of the lemma. This is probably due to the fact that the greater number of cultivated varieties are hulled and also because of the difficulty of removing the hull in order to make a study of the caryopsis.

Tschermak (36) found that the F_2 of *black* $\times$ *non-black* segregated in simple Mendelian ratio of 3 black to 1 white. This has been corroborated by many later investigators including Biffen (3), Kezer and Boyack (23), Ubisch (37), Hor (21), Robertson (31), Sigfusson (32) and Kuckuck (24). Biffen (3) noted that black versus white pericarp behaved similarly, also that black pericarp was always associated with black lemma.

The F_2 of a cross *purple* $\times$ *white* lemma was noted by Biffen (3) to segregate 3 purple to 1 white. Miyaka and Imai (26) explain their results on a 2-gene basis, P_1 and P_2 . P_1P_2 is dark purple, P_1p_2 or p_1P_2 is light purple, while p_1p_2 is white. The F_2 of the cross *dark purple* $\times$ *white* segregated 9 dark purple: 6 light purple: 1 white. The same investigators obtained results which suggest a single gene difference between blue and yellow endosperm. Kuckuck (24) found that the development of blue aleurone is dependent upon a single gene, F . The intensity of coloration is greatly affected by environmental conditions.

*A thesis submitted to the Graduate Division, University of California, in partial fulfillment of the requirements for the degree of Doctor of Philosophy, August, 1929.

†Agrostologist.

Kajanus and Berg (22) found that *yellow* × *dark violet* kernel gave a complicated segregation in F₂ and suggest two factors. A controls the blue color of the aleurone, B a brown color in the pericarp. Without A the aleurone is colorless; without B the pericarp is yellow. When both A and B are present the kernel is violet-brown.

INHERITANCE OF CHLOROPHYLL DEFICIENCIES

A number of different forms of chlorophyll deficiencies have been described. Nilsson-Ehle (29) studied the inheritance of six types, namely Albina 1, Albina 2, Albina 3, Yellow 1, Yellow 2 and Chlorina. Each of these when crossed with green showed itself to be a simple Mendelian recessive. When crossed with each other they showed a two factor difference.

Hallqvist (15, 16, 17) working with several of the same forms obtained results similar to Nilsson-Ehle.

In most chlorophyll deficient forms the development of chlorophyll is dependent upon temperature. In general, low temperature favors the reduction of color. However, the various forms will differ in their reaction to temperature. Many show a very marked color reduction even in favorable temperature conditions, and the degree of reduction in lower temperatures is more or less unchanged.

One of the mutations studied by Hallqvist behaved very differently. At a temperature between 0° and 10°C. the seedlings were white and soon died, without the development of chlorophyll. If kept at a temperature of 12°-15°C. the seedlings were white at first, but after a few days developed chlorophyll at the tip of the leaf blades. The seedlings were unable to develop far under this temperature and died at an early stage. At a temperature of 20°C. the white stage was very short and the leaves soon became green. The seedlings grew but in a "monstrous" manner. The plants were dwarfed in comparison with the normal, and they produced no bloom. The mutant first appeared in a F₂ of the cross *Gold* × *Swedish Northland*. The F₁ contained normal plants. In the F₂, five of the six families were constant and normal, the sixth segregated into 113 normal: 30 dwarfs, which suggested a 3:1 ratio.

Collins (6) reports on an albino form which shows the albino condition only when grown at a temperature below 45°F. (7.2°C.). When the albino plant is placed in a higher temperature chlorophyll is developed and the plant grows normally, finally producing seed. In this manner it is different from Hallqvist's form. When crossed with normal the F₂ segregated 3 green: 1 albino.

INHERITANCE OF OTHER CHARACTERS

Fertility of the lateral florets. Wiggan's (38) classification of the cultivated varieties of barley suggests that all varieties belong to one species, *Hordeum sativum* Jess. The species is usually divided into four main groups or subspecies on the basis of fertility of the lateral florets, viz.—

<i>Hordeum sativum vulgare</i>	lateral florets completely fertile.
" " <i>intermedium</i>	lateral florets partially fertile.
" " <i>distichon</i>	lateral florets staminate.
" " <i>deficiens</i>	lateral florets sexless.

The genetic differences causing this variation in degree of fertility or sterility of the lateral florets have been investigated perhaps more than any other set of differences in barley.

Biffen (2, 3) made reciprocal crosses between *deficiens* $\times$ *distichon vulgare* $\times$ *deficiens* and *distichon* $\times$ *vulgare*, and in each case obtained segregation in the F_2 which suggested a single factor difference.

Mackie (25) confirms Biffen's results with respect to *deficiens* $\times$ *distichon*.

Engledow (7) comes to the conclusion, based upon his own observations and those of Biffen, that *deficiens*, *distichon* and *vulgare* form an allelomorphous series with respect to fertility of the lateral florets of the spike. Dominance is in the order *deficiens*, *distichon* and *vulgare*.

Hor (21) confirms Engledow's conclusions.

Neatby (27, 28), Tedin and Tedin (33) and Robertson (31) obtain monohybrid segregation in F_2 of *vulgare* $\times$ *distichon*.

Ubisch (37) explains the difference between common 2-rowed barleys, *distichon*, and 6-rowed barleys, *vulgare*, on a two factor basis, the factor pairs being ZzWw. Z must be present in either homozygous or heterozygous form if the plant is to be 2-rowed. W produces the transitional form between the 2-rowed and 6-rowed types, that is *intermedium*. Common 2-rowed rowed has the constitution ZZWW, 6-rowed is zzww, while *intermedium* is zzWW.

Gillis (12) supports Ubisch's view in that two factors are involved between *distichon* and *vulgare*. However, he concludes that there is a third factor D for the fertility of the lateral florets. The *deficiens* forms carry the recessive d as do also the 6-rowed forms. The expression of d as absence of the lateral florets can not occur without the Z factor.

H. sativum intermedium was generally considered to be of hybrid origin and unstable, segregating into *distichon*, *intermedium* and *vulgare* forms in the ratio of 1:2:1. Harlan and Hayes (19), however, have found that when certain varieties of *distichon* and *vulgare* are crossed stable intermediate forms may be obtained. They conclude that two factors must be involved in this case. Manchuria, the 6-rowed parent, contained two factors, one for 6-rowed and one for *intermedium*, which was hypostatic to the 6-rowed factor. Crossed between *intermedium* and 6-rowed showed a one factor difference.

At present the evidence is in favor of the explanation of fertility of the lateral florets on the basis of an allelomorphous series which includes *deficiens*, *distichon* and *vulgare*. In addition there may be present modifying genes which produce stable *intermedium* forms.

Rachilla hairs. The rachilla at the base of the barley kernel is covered either with long, unbranched hairs or short, branched hairs. The investigations of Biffen (3), Ubisch (37), Engledow (7), Hor (21), Robertson (31) and Sigfusson (32) show that there is only one factor pair involved. The long haired character is dominant. Hor observed that the factor pair involved here (L1) also affects the pubescence of the outer glumes.

Hooded versus awned. In seven crosses between hooded and awned varieties Biffen (2, 3) obtained all hooded individuals in the F_1 . In two of the crosses, however, the hoods were borne on awns one-half to four inches in length. The length of these awns varied considerably in the same spike. The F_2 segregated into 3 hooded : 1 awned. In the case of the awned-hooded heterozygotes the F_2 showed considerable variation in the length of the awned-hoods but no indications could be detected of segregation into individuals with sessile hoods, and true awns only.

Thatcher (35), Kezer and Boyack (23), Hor (21), Hayes and Garber (20) and Robertson (31) confirm the above results.

Ubisch (37) explains the segregation of his crosses on a two factor basis. K is a dominant factor for hooded, A for long awns. KKAA and KKaa individuals are hooded, kkAA are long awned, and kkaa are short awned.

Adherence of lemma and palea to caryopsis. Biffen (3) found that the F_2 of a cross hulled $\times$ hullless segregated in the simple Mendelian ratio 3 hulled : 1 hullless or naked. Other investigators, Thatcher (35), Gaines (10), Ubisch (37), Hor (21), Neatby (27, 29), Tedin and Tedin (33), have confirmed Biffen's observation.

LINKAGE

According to the table compiled by Gaiser (11) and the later work of Griffiee (14), all the cultivated "species" of barley have a haploid chromosome number of 7. Theoretically, then, seven linkage groups are possible.

Linkage.

Author.

Characters linked with:—

1. *Fertility of lateral florets.*

Height of plant.	Tedin and Tedin, 1926.
Height of plant, one factor.	Neatby, 1925, 1929.
Height of plant.	Miyaki and Imai, 1922.
One factor for barbing of nerves of lemma.	Ubisch, 1919.
Length of awn.	Engledow, 1924.
One factor for length of awn.	Miyaki and Imai, 1922.
One factor for resistance to Helminthosporium.	Griffiee, 1925.
Early heading.	Griffiee, 1925; Neatby, 1926.
Extension of outer glume.	Hor, 1924; Neatby, 1929.
Density of spike.	Neatby, 1926.
One factor for purple lemma.	Miyaki and Imai, 1922.
2. *Adherence of lemma to caryopsis.*

Extent of pubescence on outer glume.	Hor, 1926.
--------------------------------------	------------
3. *Density of spike.*

Basal character of lemma.	Tedin and Tedin, 1927.
A factor for length of awn.	Ubisch, 1919.
	Miyaki and Imai, 1922.
Height of plant.	Ubisch, 1919.
One of the factors for hooded.	Miyaki and Imai, 1922.

4. *Black lemma.*
 - Texture of awn. Hor, 1924.
 - Length of rachilla hairs. Hor, 1924.
 - Color of caryopsis. Biffen, 1907.
 - One albino factor. Robertson, 1929.
 - One factor for resistance to Helminthosporium. Griffee, 1925.
5. *Hooded.*
 - One albino factor. Robertson, 1929.
 - Factor for Xantha seedlings. Robertson, 1929.
6. *Albina 3.*
 - Chlorina. Nilsson-Ehle, 1922.
 - Hallqvist 1926.
- Albina 4. Hallqvist, 1926.

There is a considerable lack of agreement with respect to the linkage relations of several factors. Hor (21) gives a cross-over value of 39.4 per cent between black versus white lemma and long versus short rachilla hairs. Robertson (31) and Sigfusson (32), with larger populations, find no linkage whatever between these two pairs of factors. Hayes and Garber (20) find independent assortment between 2- versus 6-rowed, hooded versus awned, black versus white lemma, and hulled versus naked. Considering all the data it seems that four linkage groups are fairly well established. Some of the chlorophyll deficient forms of Nilsson-Ehle and Hallqvist may form a fifth group.

Group I.

Fertility of lateral spikelet.
Height of plant.
Early heading.
Density of head.
One factor for resistance to Helminthosporium.

Length of awn.
Extension of outer glume.
Basal character of lemma.
One factor of purple lemma.

Group II.

Hooding.
One albino factor.
Xantha seedling.

Group III.

Black lemma and pericarp.
Texture of awn.
One albino factor.
One factor for resistance to Helminthosporium.

Group IV.

Covering of caryopsis.
Extent of pubescence on outer glume.

Group V.

Albina 3.
Chlorina.
Albina 4.

MATERIAL AND METHODS

All pigmentation in the caryopsis of barley is the result of two pigments, anthocyanin, which gives the red, blue and purple colors, and a melanin-like pigment, which is responsible for black. (Harlan, 18). If no pigment is present in either the aleurone layer or pericarp the caryopsis is white. If the aleurone is blue, and the pericarp colorless, it is blue. A red pericarp and colorless aleurone give a red caryopsis. A red pericarp and blue aleurone produce the purple color. Black is found only in the pericarp.

The lemma may be colored black, purple or orange. The first two are due to the same pigments which affect the caryopsis. Lack of pigment gives a white lemma.

Anthocyanin in the lemma may be confined to the veins in which case the veins are purple.

Crosses were made to determine the manner of inheritance of the various color characters and their linkage relation with other characters whose mode of inheritance has been fairly well established.

In order to make the examination of the caryopsis easier and thus the color classification more nearly correct, naked strains of barley were used almost exclusively.

Parental stocks were secured from various sources. The majority were obtained from Professor W. W. Mackie and Dr. F. N. Briggs of the University of California. Two strains were obtained from Dr. H. V. Harlan, Department of Agriculture, Washington, and one from Institut de Botanique Appliqué et d'Amélioration des Plantes, Leningrad, U.S.S.R. The remainder were selected from strains grown by the Division of Genetics, University of California.

By making use of the greenhouse and artificial light it was possible to grow three generations within fifteen months. Parental stock was sown in the greenhouse the latter part of November, 1927. During the following February and March the majority of the crosses were made. (A second series of crosses was made in September, 1928, with stock sown the previous June). The F_1 seeds were sown in the greenhouse in 6-inch pots on June 4, 1928, and the plants harvested at the end of September. The F_2 seeds were sown in 4-inch pots during the latter part of October and the early part of November. During the period December 15 to January 2, 1928, artificial light was applied from 4.30 p.m. to 10.00 p.m. daily. From January 3 to the end of the ripening period, which was about February 1, the plants were grown in continuous light. The extra light considerably hastened maturity.

F_1 and F_2 plants were examined and classified according to (a) fertility of the lateral spikelets, (b) length of pubescence on glumes, (c) length of rachilla hairs, (d) hooding and awning, (e) covering of caryopsis, (f) curving of peduncle, (g) color of lemma, (h) color of veins of lemma, (i) color of pericarp, (j) color of aleurone.

Since the aleurone characters are the result of immediate fertilization, they are a generation in advance of the other head characters which were studied. The F_2 seeds were separated according to aleurone color so that the relation of blue aleurone to other characters might be determined.

The F_2 generation of an albino-normal cross, made by Dr. J. L. Collins, was grown and studied to ascertain the inter-relation between albino and (a) fertility of lateral spikelet, (b) length of rachilla hairs, (c) color of veins of lemma and (d) color of aleurone. This albino form shows the albino condition only when grown at a temperature below 45°F. (7.2°C.). When the albino plant is placed in a higher temperature chlorophyll is developed and the plant grows normally, finally producing seed. (Collins, 6).

STATISTICAL METHODS

The significance of the deviation of the observed frequencies from normal Mendelian ratios was tested by the P.E. of each class. The general formula, $P.E. = .6745 \sqrt{n.p.q.}$, was used, where n is the total number of individuals, p is the percentage of individuals in any one class expressed as a decimal, and q is $1.0 - p$. In frequencies having more than two classes a χ^2 value was obtained as an additional test. Where irregularities in the behavior of individual characters occurred in a dihybrid ratio the observed frequencies were compared with theoretical frequencies calculated by the method outlined by G. N. Collins (5).

$$a'b' = \frac{(aB + ab)(Ab + ab)}{n}$$

$$a'B' = \frac{(aB + ab)(AB + aB)}{n}$$

$$A'b' = \frac{(AB + Ab)(Ab + ab)}{n}$$

$$A'B' = \frac{(AB + Ab)(AB + aB)}{n}$$

Where linkage apparently occurred, three methods were used in calculating the crossover value, namely Clausen's method (Hor 21, Babcock and Clausen 1), the Product Moment Correlation method (Owen 30), and Bernstein's method (4). The calculations will be given for all three when dealing with the first cases of linkage. The crossover values obtained did not always agree. Bernstein's method usually gave the lowest χ^2 .

Owen's formula.

$$r = \frac{\frac{d}{n} - q_1 q_2}{\sqrt{P_1 P_2 q_1 q_2}}$$

$$d = ab \qquad P_2 = \frac{AB - aB}{n}$$

$$P_1 = \frac{AB - Ab}{n} \qquad q_2 = \frac{Ab - ab}{n}$$

$$q_1 = \frac{aB - ab}{n} \qquad n' = \text{total population.}$$

The crossover value is obtained directly from the value of r by referring to Owen's tables. This method is particularly useful in determining linkage where more than two pairs of genes are involved.

Bernstein's formula.

$$t = \frac{-L}{2N} \pm \sqrt{\frac{L}{4N^2} - \frac{M}{N}}$$

$$t = q^2 \text{ or } 1 - p^2$$

$$q = \text{crossover value in case of repulsion} = \sqrt{t}$$

$$p = \text{coupling} = 1 - \sqrt{t}$$

$$N_1 = AB; N_2 = Ab; N_3 = aB; N_4 = ab; N = \text{total population.}$$

$$L = -N_1 + 2(N_2 + N_3) + N_4$$

$$M = -N_4$$

$$\text{Calculated proportion} = \frac{2+t}{4} : \frac{1-t}{4} : \frac{1-t}{4} : \frac{t}{4}$$

To determine the value of t , the sign before the square root is chosen so that the value of t is positive. In case of coupling this value lies between $\frac{1}{4}$ and 1.

Clausen's Method.

Per cent of crossing over =

$$(a) \quad 100 \left(1 - 2 \sqrt{\frac{a''b''}{n}} \right) \quad \text{coupling phase.}$$

$$(b) \quad 100 \times 2 \sqrt{\frac{a''b''}{n}} \quad \text{repulsion phase.}$$

$$AB : Ab : aB : ab = \text{observed} = O$$

$$A^1B^1 : A^1b^1 : a^1B^1 : a^1b^1 = \text{calculated frequency for independent assortment} = T$$

$$A''B'' : A''b'' : a''B'' : a''b'' = \text{calculated linkage proportion.}$$

$$A^1B^1 \pm \sum \frac{O - T}{4} = A''B''; + \text{ in coupling, } - \text{ in repulsion.}$$

$$A^1b^1 \pm \sum \frac{O - T}{4} = A''b''; - \text{ " " } + \text{ " "}$$

$$a^1B^1 \pm \sum \frac{O - T}{4} = a''B''; - \text{ " " } + \text{ " "}$$

$$a^1b^1 \pm \sum \frac{O - T}{4} = a''b''; + \text{ " " } - \text{ " "}$$

INDIVIDUAL CHARACTERS

COLOR OF PERICARP

Black versus not-black. (Bk. bk) The F_1 of crosses involving black versus white and black versus red pericarp was in all cases black. The F_2 segregated in the ratio of 3:1, the actual frequencies being 731 black and 257 not-black. The deviation from the theoretical is 10 and the P.E. ± 9.18 .

Red versus White Pericarp. (R.r and O.o). Apparently two genes are involved in the production of red pericarp. Crosses, in which red pericarp was crossed with white, gave an F_1 all red and F_2 which segregated 3 red to 1 white, showing a single gene difference. However, one cross, in which both parents had white pericarp, the F_1 was red and the F_2 segregated 9 red to 7 white, showing complementary factors were involved. On the basis of these results two genes are evidently necessary to produce red pericarp. O is a basic factor and necessary for the expression of R.

TABLE 1. F_2 segregation of red $\times$ white pericarp. (R.O. $\times$ r.o.).

Cross	Red	White	Total
2223 $\times$ 257	475	162	637
185 $\times$ 2277	41	21	62
3277 $\times$ 2040	24	3	27
2222 $\times$ 672-A	36	18	54
Obs.	576	204	780
Theor. 3:1	585	195	
Dev.	9.0 $\pm$ 8.15		

TABLE 2. F_2 segregation of white $\times$ white pericarp. (R.o $\times$ r.o.).

Cross	Red	White	Total
2221 $\times$ 2223	93	80	173
Theor. 9:7	97.3	75.7	
Dev.	4.3 $\pm$ 4.40		

COLOR OF ALEURONE

Blue versus White Aleurone. (Bl.bl) F_2 and F_3 segregations show a single gene difference between blue and white aleurone. The F_1 aleurone was blue and F_2 aleurone, which is on the F_1 plant, segregated 3 blue to 1 white. Theoretically the F_2 plants, bearing the F_3 aleurone, should segregate in the proportion of 1 all blue to 2 segregating (1 all blue: 2 blue and white: 1 all white) to 1 all white. However, environmental conditions make it difficult to separate the homozygous blues from the heads which are segregating. These two classes were therefore grouped together, the resulting ratio being 5 blue : 3 white.

F_2 proportion. Caryopsis	F_3 proportion. Plants.	Balanced proportion.	
1. Bl.Bl.	1 all Bl. Bl.	2 Bl.Bl	} 5 blue.
	1 Bl.Bl.	1 Bl.Bl.	
2 Bl.bl.	2 2 Bl.bl	2 Bl.bl.	
	1 bl.bl	1 bl.bl.	} 3 white
1.bl.bl	1 all bl.bl.	2 bl.bl.	

The F_2 kernels on the F_1 plants segregated 683 blue: 223 white, which is very close to a 3:1 ratio. The deviation from the theoretical is 3.5 and the P.E. $\pm$ 8.79. The F_2 plants, the kernels of which contain the F_3 endosperm, also agreed quite closely to the theoretical ratio of 5:3. Out of 857 plants 513 bore blue kernels and 344 only white. The deviation from the expected is 22.6 and the P.E. $\pm$ 9.56.

COLOR OF LEMMA

Black versus not-black. (Bk.bk). The behavior of black versus not-black lemma was the same as black versus not-black pericarp. The F_1 was black and the F_2 segregated 3 black to 1 not-black. The frequencies obtained were 905 black and 333 not-black, the deviation being 23.5, and the P.E. ± 10.26 .

Purple versus White. (P.p.). In the crosses studied purple lemma behaved as a simple dominant. The F_1 was purple. The F_2 segregated in the normal ratio of 3 purple: 1 white.

TABLE 3. F_2 segregation of purple $\times$ white lemma (P $\times$ p).

Cross	Purple	White	Total
2223 $\times$ 257	474	165	639
185 $\times$ 2277	42	23	65
3277 $\times$ 2040	24	3	27
Obs.	540	191	731
Theor. 3:1	548.25	182.75	
Dev.	8.25 $\pm$ 7.90		

White versus Orange. (Br.br). A strain of barley (6800) with orange lemma was received from the Institut de Botanique Appliqué et d'Amélioration des Plantes, Leningrad, U.S.S.R. This was crossed with a black barley and in the F_2 three lemma colors appeared—black, white, and orange. Omitting the black class the frequencies in the white and orange classes were 44 and 19 respectively. This is in quite close agreement with a 3:1 ratio, the deviation being 3.25 and the P.E. ± 2.32 . Orange color of lemma is evidently recessive to white.

COLOR OF VEINS OF LEMMA

Purple versus White Veins. (C.E. and F.). A study of the data obtained from crosses between purple and white veins indicates that probably three genes are involved in the expression of purple veins. F_2 ratios of 3:1 and 9:7 were obtained. Many of the crosses also involve P, which is linked with C and therefore the distribution in the white lemma class did not show normal 3:1 or 9:7 ratios. The linkage relations will be discussed later.

TABLE 4. F_2 segregation of purple veins $\times$ white veins (C.E.F. $\times$ c.E.F.)

Cross	Purple	White	Total
2223 $\times$ 185	46	18	64
Theor. 3:1	48	16	
Dev.	2 $\pm$ 2.34		

TABLE 5. F_2 segregation of purple veins $\times$ white veins, (C.E.F. $\times$ C.e.f.)

Cross	Purple	White	Total
2224 $\times$ 257	19	13	32
2277 $\times$ 2224	29	19	48
Obs.	48	32	80
Theor. 9:7	45	35	
Dev.	3. $\pm$ 2.99		

TABLE 6. F_2 segregation of white veins $\times$ white veins. (C.e.F. $\times$ c.E.F.).

Cross	Purple	White	Total
185 $\times$ 2222	6	4	10
2222 $\times$ 185	22	19	41
2208 $\times$ 2221	40	28	68
Obs.	68	51	119
Theor. 9:7	66.9	52.1	
Dev.	1.1 $\pm$ 3.65		

FERTILITY OF THE LATERAL SPIKELETS

Non-vulgare versus Vulgare type. ($a^s a^f$). The two-rowed parent in all crosses was a strain of *Hordeum distichon* L. In accordance with the majority of investigators non-vulgare behaved as a simple dominant. The F_1 was two-rowed and the F_2 segregated 3:1, the frequencies being 1267 non-vulgare and 479 vulgare type. The deviation is 42.5 and P.E. ± 12.2 .

LENGTH OF PUBESCENCE ON GLUMES AND HAIRS ON RACHILLA

The length of the pubescence on the empty glumes and the length of hairs on the rachilla are determined by a single gene. Long-haired rachilla was always associated with long pubescence on the glume. In over two thousand plants, the result of a number of different crosses, no exceptions to the above were found. This is in agreement with the findings of Hor (21).

Long rachilla hairs (L) when crossed with short (1) gave an F_1 with long hairs and an F_2 which segregated 3 long to 1 short. The frequencies were 1458 long and 487 short; deviation 0.75, P.E. ± 12.9 .

TERMINAL APPENDAGE OF LEMMA

Hoods versus Awns. (K.k). Hoods versus awns showed a single factor difference, the hooded condition being dominant. The F_2 of crosses involving hoods and awns segregated 1407 hooded to 487 awned, the deviation from the normal 3:1 ratio being 13.5, the P.E. ± 12.65 . However, other genes must play a rôle in the position of the hoods for different types of hooding were observed. Some were almost sessile, some on short extensions, while others appeared at the end of almost full awns. These are probably the types noted by Biffen (2, 3) and Ubisch (37).

COVERING OF THE CARYOPSIS

Hulled versus Naked. (N.n). The results of crosses involving hulled and naked grain showed a single gene difference, the naked condition being recessive to hulled. The F_1 was hulled and F_2 gave the ratio 3 hulled: 1 naked. The frequencies obtained were 290 hulled and 106 naked. The deviation is 7.0 and P.E. ± 5.81 .

CURVING OF THE PEDUNCLE

In the F_2 of several crosses it was noticed that a definite proportion of the spikes were bent over due to a curving of the peduncle just below the spike. All the parental strains were of the lax-ear type and were more or less nodding. However, in the majority of cases the bending occurred in the rachis within the spike and not in the peduncle. An examination of the parental stock showed that a few strains possessed this character.

Erect versus Curved Peduncle. (Cr.cr). Curved peduncle behaved as a simple recessive to erect. The F_2 segregated in the normal 3:1 ratio, the frequencies being 111 erect and 47 curved, which gives a deviation of 7.5 from the theoretical and a P.E. of ± 3.67 .

CHLOROPHYLL DEFICIENCY

Green versus Albino Seedling. ($Alb^t \times alb^t$). The albino strain used in this cross shows the albino condition only at temperatures below 45°F. (J. L. Collins, 6). An F_2 of the cross green $\times$ albino was grown from F_1 seed obtained from Professor Collins.

TABLE 7. F_2 segregation of green $\times$ albino. (Albt. $\times$ albt.).

Cross No.	Green	Albino	Total
27.7	176	33	209
27.10	145	44	189
Obs.	321	77	398
Theor. 3:1	298.5	99.5	
Dev.	22.5 ± 5.83		$\frac{D}{P.E.} = 3.86$

This deviation is quite large and is just within the limits where it may be said to be due to chance alone. A germination test of seed from the albino and green parental strains showed considerable difference in the viability between the two strains. The normal green strain germinated 93.1 per cent whereas the albino was only 73.3 per cent viable. By taking this difference into consideration a new theoretical frequency was used to test the observed frequency. Calculated frequency $3 \times 93.1 : 73.3 = 279.3 : 73.3$. Expressed in percentage this ratio becomes 79.22 : 20.78.

TABLE 8. F_2 segregation of green $\times$ albino. (Albt. $\times$ albt.).

	Green	Albino	Total
Observed	321	77	398
Calc. 79.22 : 20.78	315.3	82.7	
Dev.	5.7 ± 5.45		

The observed frequency is in close agreement with the calculated and one is justified in assuming a single gene difference between green and Albino^t. This confirms the previous work of Collins (6).

COMBINATIONS

I. COLOR OF PERICARP IN COMBINATION WITH OTHER CHARACTERS.

A. BLACK PERICARP

Black versus Not-black (Bk.bk) and 2-rowed versus 6-rowed.

Black pericarp is inherited independently of the fertility of the lateral spikelets. The frequencies obtained from crosses involving these two pairs of genes are in close agreement with the theoretical 9:3:3:1 ratio.

TABLE 9. F_2 segregation.

Phenotypes	2-rowed, black $\times$ 6-rowed, white		2-rowed, white $\times$ 6-rowed, black		Combined	
	Obs.	Calc.	Obs.	Calc.	Obs.	Calc.
2-rowed, black	406	408.4	131	147.4	537	555.8
" white	142	136.1	49	49.1	191	185.3
6-rowed, black	130	136.1	64	49.1	194	185.3
" white	48	45.4	18	16.4	66	61.8
Total	726	726	262	262	988	988.2
χ^2	0.71		6.55		1.47	

Black versus Not-black (Bk. bk.) and Long versus Short Rachilla Hairs. (L.l)

Black pericarp and long rachilla hairs are inherited independently of each other. The F_2 frequencies agree with the theoretical very closely, the χ^2 value being less than unity.

Black versus Not-black (Bk. bk.) and Hooded versus Awned (K.k)

Black pericarp and hooded lemma are not linked. The F_2 distribution is in accordance with the normal dihybrid ratio.

Black versus White Pericarp (Bk.bk) and Hulled versus Naked Caryopsis. (N.n)

The F_2 distribution shows independent assortment for these two pairs of genes.

TABLE 10. F_2 segregation of crosses involving black versus not-black pericarp (Bk.bk) with long versus short rachilla hairs (L.l), hooded versus awned (K.k) and hulled versus naked (N.n) respectively.

		Pericarp		Total	χ^2 9:3:3:1
		Black (Bk)	Not-black(bk)		
Rachilla hairs:—	Long (L)	443	154	793	0.26
	Short (l)	148	48		
Hooded	(K)	537	183	950	0.42
	Awned (k)	171	59		
Hulled	(N)	109	36	193	0.11
	Naked (n)	35	13		

Black versus Red Pericarp

1. ($Bk.r \times bk.R$)

F_2 data show a two gene difference between black and red pericarp, the red being hypostatic to black. The F_2 segregated in the proportion of 12 black: 3 red: 1 white.

TABLE 11. F_2 segregation of black pericarp $\times$ red pericarp. ($Bk.r \times bk.R$)

Cross	Black (Bk.R and Bk.r)	Red Bk.R	White bk.r	Total
2223 $\times$ 672A	143	36	18	197
Theor. 12:3:1	147.7	36.9	12.3	
Dev.	4.7	0.9	5.7	
P.E. $\pm$	4.1	3.7	2.29	
$\chi^2 =$	2.81			

2. ($Bk.R.I.J. \times bk.R.i.j$)

Two crosses, each having No. 2224 as the black parent, did not give the expected 12:3:1 ratio. The F_2 segregated in the ratio of 48 black: 9 white: 7 red. The 9:7 ratio in the non-black classes suggests two complementary genes (I and J) which together inhibit the expression of red pericarp. It also suggests that the black parent was homozygous for R, the gene for red pericarp. Otherwise instead of the 48:9:7 ratio a 192:43:21 ratio would occur. The observed frequencies tested against this latter ratio gives a χ^2 value of 6.91. The χ^2 value on the basis of 48:9:7 ratio is only 0.01, which is an exceptionally close fit. The close fit of the theoretical indicates independent assortment between Bk, I, and J.

TABLE 12. F_2 segregation of black pericarp $\times$ red pericarp. ($Bk.R.I.J. \times bk.R.i.j$)

Cross	Black Bk.I.J. Bk.i.J. Bk.I.j.	White bk.I.J.	Red bk.I.j. bk.i.J. bk.i.j.	Total
2277 $\times$ 2224	174	40	29	243
2224 $\times$ 257	192	29	25	246
Obs.	366	69	54	489
Theor. 48:9:7	366.8	68.8	53.5	
Dev.	0.8	0.2	0.5	
P.E. $\pm$	6.46	5.12	4.66	
$\chi^2 =$				0.008

Black versus Not-black Pericarp with Black versus Not-black Lemma.

In all the crosses involving black pericarp or lemma, black pericarp was always associated with black lemma. In almost twelve hundred plants there was no exception to this. Evidently the same gene affects the development of black pigment in both pericarp and lemma, or if two genes are responsible for the development of this pigment they must be so closely linked that crossing over is a very rare occurrence. This same condition was noted by Biffen (3).

Black versus Not-black Pericarp (Bk.bk) with Purple versus White Lemma (P.p).

The results of crosses involving black pericarp and purple lemma are identical to those obtained when black is crossed with red pericarp. (See tables 11 and 12). A two-gene difference occurs between black and purple, the F_2 ratio being 12 black: 3 purple: 1 white. I and J the complementary inhibiting genes carried by No. 2224, also affect P, the gene for purple lemma.

Black versus Not-black Pericarp or Lemma (Bk.bk) with White versus Orange Lemma. (Br.br).

Black lemma and orange lemma show a two-gene difference. The F_1 was black. The F_2 gave a normal ratio of 12 black: 3 white: 1 orange. There is no indication of linkage.

TABLE 13. F_2 segregation of black lemma $\times$ orange lemma. (Bk.Br. $\times$ bk.br).

Cross	Black	White	Orange	Total
6800 $\times$ 2208	153	44.0	19.0	216
Theor. 12:3:1	162	40.5	13.5	
Dev.	9.0	3.5	5.5	
P.E. $\pm$	4.29	3.87	2.40	
$\chi^2 =$	3.04			

Black versus Not-black Pericarp (Bk.bk) with Blue versus White Aleurone (Bl.bl).

In crosses involving black pericarp and blue aleurone the caryopsis on the F_1 plants are black. the pericarp of such grains belongs to the F_1 , while the aleurone which is beneath is F_2 . Thus the F_2 aleurone segregation is masked by the F_1 black pericarp. The heads of the F_2 plants show the F_2 pericarp and F_3 aleurone. For this reason the normal F_2 ratios are not obtained but rather a combination of F_2 and F_3 . Instead of the normal 12:3:1 ratio, the ratio 24:5:3 is used in determining the theoretical frequency. In these crosses blue segregated quite independently of black, the χ^2 values obtained being 1.82 and 1.22.

TABLE 14. F_2 segregation black versus not-black pericarp with blue versus white aleurone.

Cross	Color	Obs	Theor. 24:5:3	Dev.	P.E.	χ^2
2222 $\times$ 672-A Bk.Bl $\times$ bk.bl	Black	143	147.8	4.8	4.1	1.82
	Blue	30	30.8	0.8	3.44	
	White	24	18.5	5.5	2.76	
	Total	197				
2277 $\times$ 2224 2224 $\times$ 257 Bk.bl $\times$ bk.Bl	Black	366	366.8	0.8	6.46	1.22
	Blue	71	76.4	5.4	5.42	
	White	52	45.8	6.2	4.35	
	Total	489				

B. RED PERICARP

Red versus White Pericarp (R.r) with Two- versus Six-rowed Spike. (a^s a^f)

The F₂ data from crosses involving these two pairs of genes strongly indicate linkage.

TABLE 15. F₂ segregation of 2-rowed, white × 6-rowed, red. (a^sr × a^fR).

Cross	Two-rowed Pericarp		Six-rowed Pericarp		Total
	Red	White	Red	White	
2223 × 257	302	156	173	6	637
2222 × 672-A	23	18	13	0	54
Obs.	325	174	186	6	691
Theor. 9:3:3:1	388.7	129.6	129.6	43.2	
Dev.	63.7	44.4	56.4	37.2	
P.E. ±	8.80	6.92	6.92	4.29	
D					
P.E. =	7.23	6.42	8.15	8.67	
χ ² =	72.24				

If the 9:3:3:1 ratio is used Clausen's method (Hor, 21) cannot be applied in calculating the linkage value for the average deviation from the theoretical is greater than the calculated double recessive class. This gives a minus quantity in the adjusted proportion. The cause of the condition is found in the fact that both 2-rowed versus 6-rowed and red versus white show a variance from the normal 3:1 ratio. By using a theoretical frequency, calculated from the observed proportions, a linkage value is obtained by Clausen's method which gives an exceedingly low χ² value.

	Observed Proportions				Independent Assortment.	
	a ^s	.7221	:	.2779	a ^f	F ₂ proportion.
2- vs. 6-rowed						
red vs. white	R	.7395	:	.2605	r	
	a ^s R					= .5340
	a ^s r					= .1881
	a ^f R					= .2055
	a ^f r					= .0724
						1.0000
						Adjusted linkage ratio
Phen.	Obs.	Calc.		Dev.		
a ^s R	325	368.9940		-43.9940		324.9828
a ^s r	174	129.9771		44.0229		173.9883
a ^f R	186	142.0005		43.9995		186.0117
a ^f r	6	50.0284		-44.0284		6.0172
	691			176.0448		691.0000
			4			
				44.0112		

$$\text{Per cent of crossing over} = 100 \times 2 \sqrt{\frac{6.0172}{691}}$$

$$= 18.66 \pm 2.46^*$$

For the calculated ratio (independent assortment), $\chi^2 = 72.54$

For the adjusted linkage ratio $\chi^2 = .00006$

Bernstein's method gives approximately the same value.

$$t = - \frac{L}{2N} \pm \sqrt{\frac{L^2}{4N^2} - \frac{M}{N}}$$

$$L = - 325 + 2(174 + 186) + 6 = 401$$

$$t = - \frac{401}{1382} \pm \sqrt{\frac{160801}{1909924} - \frac{12}{691}}$$

$$= - .290159 \pm \sqrt{.101559}$$

$$= - .290159 + .318682 = .028423$$

$$q = \sqrt{t} = \sqrt{.028423} = .1686$$

$$\text{C.O. value} = 16.86 \text{ per cent.}$$

$$\chi^2 = 4.33$$

Red versus White Pericarp with Long versus Short Rachilla Hairs.

1. *L.R.O. × l.r.O.*

In this cross the parent stocks differ in L and R. The F_2 segregation shows that these two pairs of genes are inherited independently.

TABLE 16. F_2 segregation of long rachilla hairs, red pericarp × short rachilla hairs, white pericarp. (*L.R. × l.r.*)

Cross	Long rachilla hairs		Short rachilla hairs		Total
	Pericarp.		Pericarp.		
2223 × 257	Red 347	White 115	Red 128	White 48	638
Theor. 9:3:3:1	358.9	119.6	119.6	39.9	
Dev.	11.1	4.6	8.4	8.1	
P.E. ±	8.45	6.65	6.65	4.12	
$\chi^2 =$	2.75				

2. *L.R.o. × l.r.O.*

TABLE 17. F_2 segregation of long rachilla hairs, white pericarp × short rachilla hairs, white pericarp.

Cross	Long rachilla hairs		Short rachilla hairs		Total
	Red	White	Red	White	
22221 × 2223	70	65	23	13	171
Theor. 27:21:9:7	72.3	56.0	24.0	18.7	
Dev.	2.3	9.0	1.0	5.7	
P.E. ±	4.36	4.14	3.05	2.75	
$\chi^2 =$	2.26				

*P.E. calculated according to Haldane's formula.

$$.477 \sqrt{\frac{(2 + p_2)(1 - p_2)}{(1 + 2p_2)n}}$$

n = total number of individuals.

p = crossover value in case of repulsion.

$1 - p$ = crossover value in case of coupling.

The deviation from the theoretical frequency is in no case over three times the P.E. Also the χ^2 value is small. These facts would appear to indicate independent inheritance. However, since both white classes in table 17 deviate considerably from the theoretical there is also a suggestion of linkage. Owen's method, which permits the calculation of linkage values where more than two factors are involved, was applied to the observed frequencies and a linkage value of 34.65 per cent and a χ^2 of 1.55 were obtained.

	Pericarp	Red	Rachilla Hairs		Total
			Long	Short	
		Red	70	23	93
	"	White	65	13	78
			135	36	171
p_1	$= \frac{93}{171}$	$= .5439$		$p_2 = \frac{135}{171}$	$= .7895$
q_1	$= \frac{78}{171}$	$= .4561$		$q_2 = \frac{36}{171}$	$= .2105$

$$r = \frac{d}{n} = \frac{q_1 q_2}{\sqrt{P_1 P_2 q_1 q_2}} = \frac{.0760 - .0960}{\sqrt{.04122240}} = -.1333$$

C.O. = 34.65 per cent

χ^2 = 1.55

χ^2 for independent assortment = 2.26

The result indicates that either R or O is linked with L. Since R is linked with a^s (the 2-rowed factor) and L is not, (table 42), one is justified in assuming the linkage to be between L and O.

Red versus White Pericarp with Hooded versus Awned.

(1) $K.r \times k.R$

TABLE 18. F_2 segregation of hooded, white pericarp $\times$ awned, red pericarp.

Cross	Pericarp Hooded		Pericarp Awned		Total
	Red	White	Red	White	
2223 $\times$ 257	337	124	140	37	638
(a) Theor. 9:3:3:1	358.9	119.6	119.6	39.6	
	Dev. 21.9	4.4	20.4	2.9	
	P.E. $\pm$ 8.45	6.65	6.65	4.12	$\chi^2 = 5.19$
	Obs. 337	124	140	37	638
(b) Calc. (Collins)	344.67	116.33	132.23	44.67	
	Dev. 7.67	7.67	7.67	7.67	$\chi^2 = 2.44$

Table 18 gives the F_2 frequencies of a cross involving K and R. When tested against a 9:3:3:1 ratio the observed frequencies show a large deviation in the red classes. This is accounted for by the fact that the awned

class is in excess of what it should be according to a normal 3:1 ratio. When tested against a calculated frequency derived by Collins' (5) method the observed more nearly fits the calculated frequency for independent assortment, the χ^2 being 2.44. Bernstein's formula, applied to the observed data, gives a linkage value of 54.87 per cent, which indicates independent assortment.

(2) *k.R.o.* $\times$ *K.r.O*

F₂ results of this cross show that the three pairs of genes Kk, Rr and Oo, are inherited independently.

TABLE 19. F₂ segregation of awned, white pericarp $\times$ hooded, white pericarp.

Cross	Hooded Pericarp		Awned Pericarp		Total
	Red	White	Red	White	
2221 $\times$ 2223	63	60	29	19	171
Theor. 27:21:9:7	72.3	56	24.0	18.7	
Dev.	9.3	4.0	5.0	0.3	
P.E. $\pm$	4.36	4.14	3.05	2.75	
$\chi^2 = 2.53.$					

Red versus White Pericarp (R.r) with Covering of Caryopsis. (N.n)

The number of individuals in the F₂ of a cross involving these genes is too small for definite conclusions. The evidence, however, is in favor of independent inheritance.

TABLE 20. F₂ segregation of hulled, red pericarp $\times$ naked, white pericarp. (N.R. $\times$ n.r)

* Cross	Hulled Pericarp		Naked Pericarp		Total
	Red	White	Red	White	
2222 $\times$ 672-A	22	16	14	3	55
Theor. 9:3:3:1	30.9	10.3	10.3	3.4	
Dev.	8.9	5.8	3.7	0.4	
P.E. $\pm$	2.46	1.93	1.93	1.20	$\chi^2 = 6.21$

When the observed frequency is compared with the calculated frequency (Collins, 5), the χ^2 is reduced to 3.11.

Red versus White pericarp (R.r) with Straight versus Curved Peduncles. (Cr.cr.)

The color of the pericarp is evidently inherited independently of the character of the peduncle. The F₂ figures for the cross from which conclusions might be drawn are small and there is considerable deviation from the normal 9:3:3:1 ratio. The χ^2 for such a comparison is 10.88. When tested against Collins' calculated frequency the χ^2 is reduced to 0.07 which is an exceedingly close fit.

TABLE 21. F₂ segregation of straight peduncle, white pericarp $\times$ curved peduncle, red pericarp. (Cr.r $\times$ cr.R)

Cross	Straight peduncle Pericarp		Curved peduncle Pericarp		Total
	Red	White	Red	White	
185 $\times$ 2277	24	13	17	8	62
Theor. 9:3:3:1	35.8	11.6	11.6	3.9	
(a) Dev.	11.8	1.4	5.4	4.1	$\chi^2 = 10.88$
P.E. $\pm$	2.63	2.07	2.07	1.29	
Obs.	24	13	17	8	
(b) Calc. (Collins)	24.47	12.53	16.53	8.47	$\chi^2 = 0.07$
	0.47	0.47	0.47	0.47	

*Black classes omitted.

Red versus White Pericarp (R.r) with Purple versus White Lemma. (P.p).

The majority of crosses in which R and P were studied, showed a complete association of red pericarp with purple lemma. In one cross, 2223 $\times$ 257 (table 22), three plants were observed which differed in color of lemma and pericarp. Two had purple lemma and white pericarp, the other had white lemma and red pericarp. Environmental conditions have a very marked effect upon coloration of the lemma especially and it is possible that these three plants are merely wrongly classified. It would be necessary to grow an F_3 in order to determine to which classes they belong. Either R and P represent the same gene or they are very closely linked.

TABLE 22. F_2 segregation of purple lemma, red pericarp $\times$ white lemma, white

Cross	pericarp. (P.R. $\times$ p.r)				Total
	Purple lemma		White lemma		
	Pericarp		Pericarp		
	Red	White	Red	White	
2223 $\times$ 257	473	2	1	161	637
Theor. 9:3:3:1	358.31	119.44	119.44	39.81	
Dev.	114.69	117.44	118.44	121.19	
P.E. $\pm$	8.44	6.64	6.64	4.12	
χ^2 =	over 600				

Crossover percentage calculated by Clausen's method (Hor, 21) is 0.46 per cent. Bernstein's method gives almost an identical value of 0.47 per cent.

All the parental strains which had purple lemma also had red pericarp. In the cross 2221 $\times$ 2223 both parents had white lemma and white pericarp. However, in the F_2 the pericarp segregated 9 red: 7 white (see table 2) while the lemma remained white. Here red pericarp is not associated with purple lemma. One of the white parents, 2223, when crossed with purple lemma strain, 257, showed a single factor difference (see table 3). No cross has been made to determine the behavior of 2221. It would seem that there were different genes involved in the coloration of pericarp and lemma, since no purple lemmas occurred in the cross 2221 $\times$ 2223. Evidently both these strains carried the recessive gene p. 2223 shows a single factor difference with red pericarp. It would then have the constitution p.R.O, while 2221 would be p.R.o, and 257, P.R.O.

Red versus White Pericarp (R.r) with Blue versus White Aleurone. (Bl. bl)

The aleurone, being a generation in advance of the pericarp, segregates in the F_1 plant. In a cross involving red color of pericarp and blue aleurone the F_1 pericarp is red. Beneath the pericarp the aleurone shows an F_2 segregation of 3 blue to 1 white. Caryopses having blue aleurone will therefore be purple, those with white aleurone will be red. The red and purple caryopses were kept separate at the time of sowing in order that the interrelation between R and Bl might be studied.

TABLE 23. F_2 segregation of white pericarp, white aleurone $\times$ red pericarp, blue aleurone, (r.bl $\times$ R.Bl)

Cross	Blue aleurone		White aleurone		Total
	Pericarp		Pericarp		
	Red	White	Red	White	
2223 × 257	354	122	121	40	637
Theor. 9:3:3:1	358.3	119.4	119.4	39.8	
Dev.	4.3	2.6	1.6	0.2	
P.E. ±	8.44	6.64	6.64	4.12	
χ² = 0.13					

The data clearly show that R and Bl are inherited independently.

II. COLOR OF ALEURONE IN COMBINATION WITH OTHER CHARACTERS.

Blue versus White Aleurone (Bl.bl) with 2- vs. 6-rowed spike. (a^s a^f).

The results obtained from crosses involving these two pairs of characters show that the genes responsible for these characters are inherited independently (see table 24).

TABLE 24. *F₂ segregation of crosses involving blue vs. white aleurone (Bl. bl) with 2- vs. 6-rowed (a^s a^f), long vs. short rachilla hairs (L.l), straight vs. curved peduncle (Cr.cr), and purple vs. white lemma (P.p) respectively.*

	Aleurone		Total	χ^2	
	Blue(Bl)	White(bl)		Collins	9:3:3:1
2-rowed (a ^s)	373	155	714	0.13	6.61
6-rowed (a ^f)	134	52			
Rachilla Hairs:—					
Long (L)	353	113	642		3.77
Short (l)	125	51			
Peduncle:—					
Straight (Cr)	34	14	64		1.77
Curved (cr)	10	6			
Lemma:—					
Purple (P)	347	120	641		
White (p)	132	42			1.68

Blue versus White Aleurone (Bl.bl) with Long versus Short Rachilla Hairs. (L.l)

No linkage occurs between the color of the aleurone and the length of rachilla hairs. The F_2 segregation of a cross L.L.B1.B1. $\times$ l.l.bl.bl. was in quite close agreement with the normal 9:3:3:1 ratio, the χ^2 being 3.77 (see table 24).

Blue versus White Aleurone (Blbl) with Hooded versus Awned. (K.k).

Table 25 gives the result of the F_2 segregation of two crosses involving color of aleurone and gene for hooding.

TABLE 25. *F₂ segregation of hooded, white aleurone $\times$ awned, blue aleurone. (k.bl $\times$ k.Bl)*

Cross No.	Hooded Aleurone		Awned Aleurone		Total
	Blue	White	Blue	White	
2223 $\times$ 257	331	136	144	31	642
2223 $\times$ 285	37	19	13	3	72
Obs.	368	155	157	34	714
Theor. 9:3:3:1	401.6	133.9	133.9	44.6	
Dev.	33.6	21.1	23.1	10.6	
P.E. $\pm$	8.94	7.03	7.03	4.36	
$\chi^2 = 12.64$					

While the deviations of the observed frequencies from the theoretical are in no case four times the P.E., there is a strong suggestion of linkage. The middle classes are high and the end classes are low, which is the condition found in repulsion.

Linkage values were obtained by several methods. These values are as follows:—

Method	Linkage value %	χ^2 value
Clausen (Hör 21)	35.4 $\pm$ 2.51	6.24
Owen (30)	40.1	2.32
Bernstein (4)	40.56	2.26

The observed frequencies when tested against calculated frequencies for consecutive theoretical linkage ratios gave a minimum χ^2 of 2.23 at a linkage value of 41.0 per cent.

Blue versus White Aleurone (Bl.bl) with Hulled versus Naked Caryopsis. (N.n)

Parental strain No. 2222 is naked and has a black pericarp and blue aleurone. When crossed with 672-A, a hulled strain having red pericarp and white aleurone, the F_1 pericarp was black and masked the F_2 segregation of aleurone color. In the F_2 plants the aleurone character showed an F_3 segregation in the non-black classes. Since neither covering of the caryopsis nor color of aleurone is linked with black (see tables 10, 14), it should be possible to ascertain the interrelation of the two former characters from a study of the non-black classes. The figures in table 26 are for the non-black classes only.

TABLE 26. F_2 segregation of hulled, white aleurone $\times$ naked, blue aleurone.

Cross	(N. bl $\times$ n.Bl)		Naked Aleurone		Total
	Hulled Aleurone	White	Blue	White	
2222 $\times$ 672-A	19	19	12	5	55
Theor.	25.8	15.5	8.6	5.2	
Dev.	6.8	3.5	3.4	0.2	
P.E. $\pm$	2.50	2.25	1.82	1.46	
$\chi^2 = 3.93$					

The total number of plants is perhaps too small to make definite statements. However, the figures in general suggest independent assortment.

Blue versus White Aleurone (Bl.bl) with Straight versus Curved Peduncle (Cr. cr)

The F_2 of the cross cr.bl. $\times$ Cr.Bl. is in close agreement with a 9:3:3:1 ratio, indicating that color of aleurone is in no way linked with curving of the peduncle (see table 24).

Blue versus White Aleurone (Bl.bl) with Purple versus White Lemma. (P.p)

Bl.bl and P.p are inherited independently of each other. The F_2 distribution of a cross involving these genes is in quite close agreement with a normal 9:3:3:1 ratio (see table 24).

III. COLOR OF LEMMA IN COMBINATION WITH OTHER CHARACTERS.

A. PURPLE LEMMA (P)

Purple vs. White Lemma (P.p) with Two- vs. Six-rowed Spike. (a^s a^f).

Table 27 gives the F_2 distribution of crosses involving purple lemma and fertility of lateral spikelets.

TABLE 27. F_2 segregation of two-rowed, white lemma $\times$ six-rowed, purple lemma. (a^s p $\times$ a^f P)

Cross	Two-rowed		Six-rowed		Total
	Purple	White	Purple	White	
2223 $\times$ 257	303	157	171	8	639
*2222 $\times$ 672-A	23	18	13	0	54
Obs.	326	175	184	8	693
Theor. 9:3:3:1	389.8	129.9	129.9	43.3	
Dev.	63.8	46.1	54.1	35.3	
P.E. $\pm$	8.81	6.93	6.93	4.30	
D					
P.E. =	7.24	6.65	7.81	8.21	$\chi^2=78.12$

*Black classes excluded.

The data strongly indicate linkage. Because of the variance from the 3:1 ratio of both two- versus six-rowed and purple versus white, a correction (see p. 474) was made in Clausen's method when determining the linkage value. The values obtained by the various methods applied are as follows:—

Method	Linkage value %	χ^2 value
Clausen (corrected)	21.52 $\pm$ 2.42	5.01
Owen	12.5	14.75
Bernstein	19.38	4.68

The observed frequencies gave a minimum χ^2 value of 4.46 when tested against a calculated frequency for 20 per cent crossing over. The linkage value for a^s -P is therefore probably between 19 and 21 per cent.

Purple versus White Lemma (P.p) with Long versus Short Rachilla Hairs. (L.l).

No linkage was observed between P and L. The F_2 distribution of a cross involving P and L showed independent assortment (table 28).

Purple versus White Lemma (P.p) with Hooded versus Awned (K,k).

The data given in table 28 show that P and K are inherited independently.

Purple versus White Lemma (P.p) with Hulled versus Naked. (N.n).

The only cross available for the study of these characters was 2222 $\times$ 672-A. 2222 is black. With respect to lemma color the F_2 segregated in the proportion of 12 black; 3 purple: 1 white. The inheritance of P and N was studied by excluding the black classes. This left a small population, consequently the evidence is not as decisive as from a larger population. The data indicate however, that P and N are inherited independently (see table 28).

Purple versus White Lemma (P.p) with Straight versus Curved Peduncle. (Cr.cr).

The F_2 distribution shows considerable variance from the 9:3:3:1 ratio. However when the observed is compared with a calculated frequency (Collins 5) there is a very close agreement, the χ^2 value being reduced from 10.06 to 0.20. Considering the small population it is very probable that P and Cr. are inherited independently (see table 28).

TABLE 28. F_2 segregation of crosses involving purple vs. white lemma (P.p) with long vs. short rachilla hairs (L.l), hooded vs. awned (K.k), hulled vs. naked (N.n), and straight vs. curved peduncle (Cr.cr) respectively.

	Lemma			χ^2	χ^2
	Purple(P)	White(p)	Total	Collins	9:3:3:1
Rachilla hairs:—					
Long (L)	337	126	635	0.04	4.40
Short (l)	124	48			
Hooded (K)	325	138	637	2.91	6.11
Awned (k)	134	40			
Hulled (N)	22	14	54	4.36	7.85
Naked (n)	16	2			
Peduncle:—					
Straight (Cr)	25	15	65	0.20	10.06
Curved (cr)	17	8			

B. ORANGE LEMMA (br)

White versus Orange Lemma (Br.br) with Long versus Short Rachilla Hairs. (L.l).

The only available material for the study of these characters is from

the cross 6800 $\times$ 2208. 6800 has long rachilla hairs and orange lemma; 2208 has short hairs and black lemma. With respect to lemma color the F_2 segregated in the proportion of 12 black: 3 white: 1 orange. In table 29 the black classes have been excluded.

TABLE 29. F_2 segregation of long rachilla hairs, orange lemma $\times$ short hairs, white lemma. (*L. br* $\times$ *l.Br*).

Cross	Long rachilla hairs Lemma		Short rachilla hairs Lemma		Total
	White	Orange	White	Orange	
6800 $\times$ 2208	29	15	13	3	60
Theor. 9:3:3:1	33.8	11.2	11.2	3.8	
Dev.	4.8	3.8	1.8	0.8	
P.E.	$\pm$ 2.59	2.04	2.04	1.26	
$\chi^2 =$	2.34				

While the observed frequency fits quite closely the frequency for independent assortment, there is a suggestion of linkage. The centre classes of the observed are higher and the end classes lower than those of the theoretical frequency. Owen's method gives a crossover value of 37.68 per cent with a χ^2 of 1.01. When Bernstein's method is used the crossover value is 39.11 per cent with a χ^2 of 0.98. A minimum χ^2 value of 0.98 was obtained when the observed frequencies were tested against crossover values of 39 and 40 per cent. When the small population is taken into consideration it is quite possible that Br. and L are loosely linked.

White versus Orange Lemma (Br.br) with Hooded versus Awned (K.k) and with Hulled versus Naked. (N.n).

The data given in table 30 show that Br. is inherited independently of both K and N.

TABLE 30. F_2 segregation of crosses involving white versus orange lemma (*Br.br*) with hooded versus awned (*K.k*) and hulled versus naked (*N.n*) respectively.

	Lemma		Total	χ^2 9:3:3:1 0.61
	White (Br)	Orange (br)		
Hooded (K)	33	13	62	
Awned (k)	11	5		
Hulled (N)	26	12	52	1.11
Naked (n)	10	4		

IV. COLOR OF VEINS OF LEMMA IN COMBINATION WITH OTHER CHARACTERS.

A number of the crosses involving the genes for veins also include Bk and P. The latter genes mask the F_2 segregation of vein color. In the data presented the black and purple lemma classes will be excluded unless specifically stated.

Three genes, C, E, and F are necessary for the production of purple veins (see tables 4, 5, 6). In determining linkage relations where more than two genes are involved Owen's method (30) will be used.

*Color of veins with Two- versus Six-rowed Spike. (*a^s a^f*)*

(1) *a^f.c.e.F* $\times$ *a^s.C.E.F*

TABLE 31. F_2 segregation of six-rowed, white veins $\times$ two-rowed, purple veins.

Cross	Two-rowed Veins		Six-rowed Veins		Total
	Purple	White	Purple	White	
2208 $\times$ 2221	34	16	6	12	68
Theor. 27:21:9:7	28.7	22.3	9.6	7.4	
Dev.	5.3	6.3	3.6	4.6	
P.E.	$\pm$ 2.75	2.61	1.93	1.74	
$\chi^2 =$	6.97				

The observed frequencies show considerable deviation from the theoretical, the χ^2 being 6.97. The parental types are in excess and a corresponding reduction occurs in the recombination classes. Owen's method gives a crossover value of 22.19 per cent. When tested against the calculated frequency for this crossover value the observed frequency is in very close agreement, the χ^2 being 0.39. Either C or E is linked with a^s .

(2) $a^s.C.e.f. \times a^f.C.E.F.$

The F_2 distribution shown in table 32 agrees very closely with the calculated distribution for independent assortment. Therefore E and F are not linked with a^s . Linkage was observed in table 31. This leads to the conclusion that C is linked with a^s .

TABLE 32. F_2 segregation of two-rowed, white veins $\times$ six-rowed, purple veins.

Cross	Two-rowed Veins		Six-rowed Veins		Total
	Purple	White	Purple	White	
3277 $\times$ 2224	22	16	7	3	48
2224 $\times$ 257	14	10	3	3	30
Obs.	36	26	10	6	78
Theor. 27:21:9:7	32.9	25.9	11.0	8.5	
Dev.	3.1	0.1	1.0	2.5	
P.E. $\pm$	2.94	2.80	2.06	1.85	
$\chi^2 =$	1.12				

Color of Veins of Lemma with Long versus Short Rachilla Hairs. (L.l).

TABLE 33. F_2 segregation of long hairs, purple veins $\times$ short hairs, white veins. (L.C.E.F. $\times$ l.C.e.f.).

Cross	Long rachilla hairs. Veins		Short rachilla hairs. Veins		Total
	Purple	White	Purple	White	
2277 $\times$ 2224	23	15	6	4	48
2224 $\times$ 257	14	9	5	4	32
Obs.	37	24	11	8	80
Theor. 27:21:9:7	33.75	26.25	11.25	8.75	
Dev.	3.25	2.25	0.25	0.75	
$\chi^2 =$	0.57				

The very close agreement of the observed to the theoretical distribution indicated that L, E and F are inherited independently.

Color of Veins of Lemma with Hooded versus Awns. (K.k)

TABLE 34. F_2 segregation of awned, purple veins $\times$ hooded, white veins. (k.C.E.F. $\times$ K.C.e.f.).

Cross	Hooded Veins		Awned Veins		Total
	Purple	White	Purple	White	
2277 $\times$ 2224	21	16	8	3	48
2224 $\times$ 257	15	7	4	6	32
Obs.	36	23	12	9	80
Theor. 27:21:9:7	33.75	26.25	11.25	8.95	
Dev.	2.25	3.25	0.75	0.25	
$\chi^2 =$	0.63				

E. and F show no linkage with K.

*Color of Veins of Lemma with Hulled versus Naked. (N.n)*TABLE 35. F_2 segregation of hulled, purple veins $\times$ naked, white veins. (N.C.E.F. $\times$ n.c.e.F)

Cross	Hulled Veins		Naked Veins		Total
	Purple	White	Purple	White	
6800 $\times$ 2208	21	11	6	4	42
Theor. 27:21:9:7	17.7	13.8	5.9	4.6	
Dev.	3.3	0.1	2.8	0.6	
P.E. $\pm$	2.16	1.51	2.05	1.36	
$\chi^2 =$	1.25				

N, C and E are inherited independently.

*Color of Veins with Straight versus Curved Peduncle. (Cr.cr).*TABLE 36. F_2 segregation of curved peduncle, purple veins $\times$ straight peduncle, white veins. (cr.C.E.F. $\times$ Cr.c.E.F.)

Cross	Straight peduncle Veins		Curved peduncle Veins		Total
	Purple	White	Purple	White	
2223 $\times$ 185	35	13	12	4	64
3277 $\times$ 2040	17	2	7	1	27
Obs.	52	15	19	5	91
Theor. 9:3:3:1	51.2	17.1	17.1	5.7	
Dev.	0.8	2.1	1.9	0.7	
P.E. $\pm$	3.19	2.51	2.51	1.56	
$\chi^2 =$	0.56				

The close agreement of the observed to the theoretical distribution indicates the independent inheritance of Cr and C.

Color of Veins with Purple versus White Lemma (P.p).

P affects the color of the whole lemma, including the veins. Thus plants having the genetic constitution CCPP, CcPP, CCpP, ccPP, and ccpP are indistinguishable.

(1) $p.c.E.F. \times P.C.E.F.$ TABLE 37. F_2 segregation of white lemma, white veins $\times$ purple lemma, purple veins.

Cross	Purple lemma	White lemma Veins		Total
		Purple	White	
185 $\times$ 2277	42	13	10	65
3277 $\times$ 2040	24	1	2	27
Obs.	66	14	12	92
Theor. 12:3:1	69.0	17.5	5.75	
Dev.	3.0	3.25	6.25	
P.E. $\pm$	2.80	2.53	1.57	
$\chi^2 =$	7.54			

Considering the white lemma classes only there is an excess in the parental class and a corresponding reduction in the recombination class. This suggests linkage.

The crossover values obtained are as follows:—

Clausen's method 37.42%; $\chi^2 = 1.88$

Bernstein's method 34.34%; $\chi^2 = 0.63$

(2) *p.C.e.F.* × *P.C.E.F.*TABLE 38. *F*₂ segregation of white lemma, white veins × purple lemma, purple veins.

Cross	Purple lemma	White lemma Veins		Total
		Purple	White	
2222 × 672-A	36	12	6	54
Theor. 12:3:1	40.5	10.1	3.4	
Dev.	4.5	1.9	2.6	
P.E. ±	2.15	1.93	1.20	
$\chi^2 =$	2.85			

The population is too small for definite conclusions but in general the evidence points towards the independent inheritance of P. and E.

(3) *P.C.E.F.i.j.* × *P.C.e.f.I.J.*

In these crosses two sets of complementary genes are involved, viz. C.E.F. and I.J. P. and C are common to all parental strains. I and J together inhibit the expression of P; if either I or J is in the recessive form the lemma is purple. The *F*₂ segregation of E and F is visible only in the white lemma classes. The normal ratio is therefore modified from 81:63:63:49 to 81:63:112.

TABLE 39. *F*₂ segregation of purple lemma, purple veins × white lemma, white veins.

Cross	White lemma Veins		Purple lemma	Total
	Purple	White		
2277 × 2224	29	19	27	75
2224 × 257	19	13	26	58
Obs.	48	32	53	133
Theor. 81:63:112	42.08	32.73	58.19	
Dev.	5.92	0.73	5.19	
P.E. ±	3.62	3.35	3.86	$\chi^2 = 1.31$

The observed agrees very well with the theoretical distribution, which indicates that E, F, I, and J are all inherited independently.

*Color of Veins with Red versus White Pericarp. (R.r).**r.c.E.F.* × *R.C.E.F*

Red pericarp is almost always associated with purple lemma. Because of the masking effect of the purple lemma the *F*₂ segregation of color of veins could not be determined in the red pericarp classes. The *F*₂ distribution was therefore in the ratio of 12:3:1 instead of 9:3:3:1.

In this cross the parents differ only in two pairs of genes viz. R and C.

TABLE 40. *F*₂ segregation of white pericarp, white veins × red pericarp, purple veins.

Cross	Red pericarp	White pericarp Veins		Total
		Purple	White	
185 × 2277	41	12	9	62
2277 × 2040	24	1	2	27
Obs.	65	13	11	89
Theor. 12:3:1	66.75	16.7	5.6	
Dev.	1.75	3.7	5.4	
P.E. ±	2.76	2.62	1.54	
$\chi^2 =$	6.08			

Considering the white pericarp classes there is an excess in the parental class and a reduction of plants in the recombination class, which suggests linkage. Clausen's method gives a crossover percentage of 36.40 and a χ^2 of 0.50. By Bernstein's method the crossover percentage is 33.73 and the χ^2 value is 0.22.

Color of Veins with Blue versus White Aleurone. (Bl.bl).

C.E.F.bl × c.E.F.Bl

TABLE 41. F_2 segregation of white aleurone, purple veins × blue aleurone, white veins.

Cross	Blue aleurone Veins		White aleurone Veins		Total
	Purple	White	Purple	White	
2223 × 185	34	10	14	6	64
Theor. 9:3:3:1	36	12	12	4	
Dev.	2	2	2	2	
P.E. ±	2.68	2.11	2.11	1.31	
χ^2	= 1.77				

The close fit of the observed to the theoretical frequency indicates independent assortment between C and Bl.

V. TWO- VS. SIX-ROWED IN COMBINATION WITH OTHER CHARACTERS.

The F_2 segregation of crosses involving two-versus six-rowed (a^s a^f) with long versus short rachilla hairs (L.l), hooded versus awned (K.k), hulled versus naked (N.n), and straight versus curved peduncle (Cr.cr) respectively is given in table 42.

TABLE 42.

	<i>Spike</i>		Total	Collins	9:3:3:1
	Two-rowed (as)	Six-rowed (af)			
Rachilla hairs:—					
Long (L)	678	264	1275	0.31	5.73
Short (l)	245	88			
Hooded (K)	665	258	1225	0.32	5.71
Awned (k)	229	83			
Hulled (N)	113	27	197	0.69	3.88
Naked (n)	43	14			
Peduncle:—					
Straight (Cr)	33	15	64	1.82	6.33
Curved (cr)	8	8			

The data show that the genes a^s a^f are inherited independently of the genes L.l, K.k, N.n, and Cr.cr.

VI. LONG VS. SHORT RACHILLA HAIRS IN COMBINATION WITH OTHER CHARACTERS.

Length of rachilla hairs is inherited independently of hooding, covering of caryopsis, and curving of the peduncle (table 43).

TABLE 43. F_2 segregation of crosses involving long versus short rachilla hairs (L.l) with hooded versus awned (K.k), hulled versus naked (N.n), and straight versus curved peduncle (Cr.cr) respectively.

	Rachilla hairs.		Total	χ^2 9:3:3:1
	Long	Short		
Hooded	1055	347	1896	1.20
Awned	369	125		
Hulled	111	38	199	0.43
Naked	40	10		
Peduncle straight	35	13	64	3.11
“ curved	15	1		

VII. HOODED VERSUS AWNED IN COMBINATION WITH OTHER CHARACTERS.

TABLE 44. F_2 segregation of crosses involving hooded versus awned ($K.k$) with hulled vs. naked ($N.n$) and straight vs. curved peduncle ($Cr.cr$).

	Lemma		Total	χ^2 9:3:3:1 0.27
	Hooded (K)	Awned (k)		
Hulled (N)	111	40	199	
Naked (n)	36	12		
Peduncle straight (Cr)	38	10	64	1.78
“ curved (cr)	10	4		

The genes $K.k$ show independent assortment with $N.n$ and $Cr.cr$.

VIII. NORMAL VERSUS ALBINO^t IN COMBINATION WITH OTHER CHARACTERS.

In all the combinations, which were studied the albino classes were considerably smaller than they should be on the basis of a normal distribution. This is partly accounted for by the difference in viability of normal and albino kernels, a condition which has been mentioned previously. Also a number of the albino plants failed to produce heads. This caused a further reduction in the albino classes, since each character used in combination with albino concerned some feature of the spike.

Normal versus Albino^t ($Alb^t.alb^t$) with Two- versus Six-rowed. ($a^s.af$).

TABLE 45. F_2 segregation normal, two-rowed $\times$ albino, six-rowed. ($a^s.Alb^t \times af.alb^t$)

Cross No.	Green		Albino		Total
	Two-rowed	Six-rowed	Two-rowed	Six-rowed	
27.7	113	59	21	4	197
27.10	108	38	24	12	182
Obs.	221	97	45	16	397
Calc. (Collins)	223.19	94.81	42.81	18.19	
Dev.	2.19	2.19	2.19	2.19	
$\chi^2 =$	0.44				

When a calculated frequency, derived by Collins' (5) method is used as a basis of comparison the observed distribution agrees very closely with the theoretical for independent assortment. If only the albino classes are considered the frequencies observed for two-rowed and six-rowed are almost in a perfect 3:1 ratio. This confirms Collins' (6) statement that Albino^t was inherited independently of number of rows in the spike.

Normal versus Albino^t ($Alb^t.alb^t$) with Long versus Short Rachilla Hairs. ($L.l$)

TABLE 46. F_2 segregation of long hairs, normal $\times$ short hairs, albino. ($L.Alb^t. \times l.alb^t$)

Cross No.	Green Rachilla Hairs		Albino. Rachilla Hairs		Total
	Long	Short	Long	Short	
27.7	125	47	17	8	197
27.10	109	37	27	9	182
Obs.	234	84	44	17	379
(a) Calc. (Collins)	233.3	84.7	44.7	16.3	
Dev.	0.7	6.7	0.7	0.7	
(b) Calc. 3:1 for Green and Albino Classes	238.5	79.5	45.75	15.25	
Dev.	4.5	4.5	1.75	1.75	
P.E. $\pm$	5.21		2.28		$\chi^2 = 0.60$

The above data show that alb^t and L are inherited independently.

Normal versus Albino^t (Alb^t.alb^t) with Purple versus White Veins of Lemma. (C.E.F. series).

TABLE 47. F_2 segregation of green, purple veins $\times$ albino, white veins.

Cross No.	Green Veins.		Albino. Veins.		Total
	Purple	White	Purple	White	
27.7	113	59	15	10	197
27.10	107	39	24	12	182
Obs.	220	98	39	22	397
(a) Calc. (Collins)	217.35	100.65	41.65	19.35	
Dev.	2.65	2.65	2.65	2.65	$\chi^2 = 0.63$
(b) Calc. 3:1 for green and albino classes	238.5	79.5	45.75	15.25	
Dev.	18.5	18.5	6.75	6.75	$\chi^2 = 8.88$
P.E. $\pm$	5.97		2.28		
(c) Calc. 9:7 for green and albino classes	178.9	139.1	34.3	26.7	
Dev.	41.1	41.1	4.7	4.7	
P.E. $\pm$	5.97		2.61		$\chi^2 = 23.04$

The data indicate that there is no linkage between alb^t. and C,E or F. With respect to the C.E.F. series, the albino parent is recessive in probably only one of these genes since the 3:1 ratio gives a much lower χ^2 value than the 9:7.

By using the albino class only the interrelation between color of veins and two- versus six-rowed was studied. Since C is linked with a^s, the gene for two-rowed (see table 31), a crossover value should be obtained if C is the gene concerned.

	Two-rowed Veins		Six-Rowed Veins		Total
	Purple	White	Purple	White	
Obs.	28	17	11	5	61
Calc. (Collins)	28.8	16.2	10.2	5.8	
Dev.	0.8	0.8	0.8	0.8	$\chi^2 = 0.22$

The distribution shows no evidence of linkage, indicating that E or F is the gene which determines the color of veins in this case.

Normal versus Albino^t (Alb^t.alb^t) with Blue versus White Aleurone.(Bl.bl)

F_2 plants were studied for aleurone color, consequently the ratio of blue: white was 5:3 instead of 3:1.

TABLE 48. F_2 segregation of normal, white aleurone $\times$ albino, blue aleurone. (Alb^t. bl $\times$ alb^t.Bl)

Cross No.	Green Aleurone		Albino. Aleurone		Total
	Blue	White	Blue	White	
27.7	105	67	15	10	197
27.10	96	50	22	12	180
Obs.	201	117	37	22	377
Theor. 5:3 in green and albino classes	198.75	119.25	36.87	22.13	
Dev.	2.25	2.25	0.13	0.13	
P.E. $\pm$	5.81		2.51		$\chi^2 = 0.07$

The close agreement of the observed distribution to the calculated indicates independent assortment between Alb^t and Bl.

LINKAGE.

Linkage was observed between one of the pairs of genes (C.c) responsible for the development of purple veins in the lemma and the genes for two-versus six-rowed spike ($a^s a^f$), red versus white pericarp (R.r), and purple versus white lemma (P.p).

The crossover values obtained are:—

C	—	P	=	34.34	per cent.
C	—	R	=	33.73	"
a^s	—	C	=	22.19	"
a^s	—	R	=	19.38	"
a^s	—	P	=	16.86	"
R	—	P	=	0.47	"

From these values the order of genes could be either C— a^s —R—P or C— a^s —P—R. The latter order is derived by considering the values obtained for a^s —C, a^s —P, and a^s —R. This is probably the correct order, since the summation of smaller values usually gives more accurate results than larger values such as between C—P or C—R.

Long versus short rachilla hairs (L.l) showed loose linkage with one of the gene pairs (O.o) responsible for development of red pericarp and the genes for white versus orange lemma (Br.br).

L—O	=	34.65	per cent	L—Br	=	39.11	per cent
-----	---	-------	----------	------	---	-------	----------

The order of genes cannot be determined from the present data since no cross was made that would permit a study of the linkage between Br. and O. Hor (21) found linkage between long versus short rachilla hairs (L.l) and black versus white lemma (Bk.bk). In the present study, with a much larger population, no linkage whatever was obtained between these genes; Robertson (31) and Sigfusson (32) also found independent assortment between L.l and Bk.bk.

Loose linkage was observed between hooded versus awned (K.k) and blue versus white aleurone (Bl.bl), the crossover value being 40.56 per cent.

Two-rowed versus six-rowed ($a^s a^f$), long versus short rachilla hairs (L.l), hooded versus awned (K.k), hulled versus naked (N.n), one of the gene pairs (E.e) involved in the development of purple veins, and black versus white pericarp and lemma (Bk.bk) are inherited independently of each other. This is suggestive of six linkage groups.

Group I.

A. $a^s a^f$ —allelomorphic series—*deficiens*, *distichon*, *vulgare*.

C.c—one of the three gene pairs concerned with development of purple veins.

R.r—one of the two gene pairs concerned with development of red pericarp.

P.p—purple versus white lemma.

Group II.

L.l—long versus short rachilla hairs.

O.o—one of the two gene pairs concerned with development of the red pericarp.

Br.br.—white versus orange lemma.

Group III.

K,k—hooded versus awned lemma.

Bl.bl—blue versus white aleurone.

Group IV.

N.n—hulled versus naked caryopsis.

Group V.

E.e—one of the three gene pairs concerned with development of purple veins.

Group VI.

Bk.bk—black versus white lemma and pericarp.

The interrelation of the following genes has been determined:—

I.i and J.j the complementary genes inhibiting P and R, show independent assortment with each other and with $a^s.a^f$ L.l, K.k, E.e, Bk.bk, and F.f. The behavior of I.i, and J.j with N.n has not been studied.

F.f, one of the three gene pairs involved in the development of purple veins, is inherited independently of $a^s.a^f$, L.l, K.k, E.e, I.i, J.j. It has not been tested with N.n or Bk.bk.

Straight versus curved peduncle (Cr.cr) is inherited independently of $a^s.a^f$, L.l, and K.k. Combinations with N.n, E.e and Bk.bk are lacking.

Normal versus albino^t ($Alb^t.alb^t$) shows independent assortment with $a^s.a^f$, L.l, and Bl.bl. No combinations with N.n, E.e, or Bk.bk were made.

SUMMARY

The inheritance of color in the caryopsis and lemma and the relation of these characters to several other plant characters have been studied.

1. The following gene pairs gave a simple Mendelian ratio in the F_2 :—two-versus six-rowed ($a^s.a^f$), long versus short rachilla hairs (L.l), hooded versus awned (K.k), hulled versus naked (N.n), straight versus curved peduncle (Cr.cr), black versus white lemma and pericarp (Bk.bk), white versus orange lemma (Br.br), purple versus white lemma (P.p), blue versus white aleurone (Bl.bl), normal versus albino seedling ($Alb^t.alb^t$).
2. Red versus white pericarp was found to be dependent upon two pairs of genes (R.r and O.o) both of which must be present in the dominant form for the development of red pericarp. One of these pairs (O.o) may possibly be necessary for the development of P, the gene for purple lemma.
3. Complementary genes (I.i and J.j) were found which together in the dominant form inhibited the expression of R and P.
4. Three pairs of genes (C.c, E.e, and F.f) are involved in the development of purple veins in the lemma. All three must be present in the dominant form for the expression of color.
5. Three linkage groups are established, namely C—A—P—R, L—O—Br, and K—Bl. It is very probable that N.n, E.e and Bk.bk represent three additional groups.

6. Five other gene pairs were studied, viz. I.i, J.j F.f, Cr.cr, Alb^t.alb^t, but insufficient data made it impossible to determine to which group they belong.

ACKNOWLEDGEMENTS

The writer wishes to express his appreciation to Professor E. B. Babcock, Dr. R. E. Clausen and Dr. J. L. Collins for their kindly interest and many helpful suggestions throughout the course of this investigation. Thanks are also due to Professor W. W. Mackie and Dr. F. N. Briggs, who so generously supplied seed of many of the parental strains used in this study.

LITERATURE CITED

1. BABCOCK, E. B. and CLAUSEN, R. E. Genetics in relation to agriculture. 2 edit. 673pp. New York. McGraw-Hill Book Co. 1927.
2. BIFFEN, R. N. The inheritance of sterility in the barleys. Jour. Agric. Sci. 1: 250-257. 1905.
3. ———. The hybridization of barleys. Jour. Agric. Sci. 2: 183-206. 1907.
4. BERNSTEIN, F. Variations und Erblchkeitsstatistik. Handb. d. Vererbungsw. Lief. 8 (1.c): 1-96. 1929.
5. COLLINS, G. N. Measurement of linkage values. Jour. Agric. Res. 27: 881-891. 1924.
6. COLLINS, J. L. A low temperature type of albinism in barley. Jour. Hered. 18: 331-334. 1927.
7. ENGEDOW, F. L. Inheritance in barley. 1. The lateral florets and the rachilla. Jour. Gen. 10: 93-108. 1920.
8. ———. II. The awn and lateral floret. Jour. Agr. Sci. 11: 159-196. 1921.
9. ———. III. The awn and lateral floret: fluctuation: a linkage: multiple allelomorphs. Jour. Gen. 14: 40-87. 1924.
10. GAINES, E. F. Inheritance in wheat, barley and oat hybrids. Wash. Agr. Exp. Sta. Bull. 135. 1917.
11. GAISER, L. O. A list of chromosome numbers in Angiosperms. Genetica 8: 401-484. 1926.
12. GILLIS, M. C. A genetical study of the fertility of the lateral florets of the barley spike. Jour. Agric. Res. 32: 367-390. 1926.
13. GRIFFEE, F. Correlated inheritance of botanical characters in barley, and manner of reaction to *Helminthosporium sativum*. Jour. Agric. Res. 30: 915-933. 1925.
14. ———. Chromosome number in species of *Hordeum*. Minn. Stud. Pl. Sci., Stud. in Biol. Sci. No. 6: 319-331. 1927.
15. HALLQVIST, C. Gametenelimination bei der Spaltung einer zweighaften und chlorophylldefekten Gerstensippe. Hereditas 4: 191-205. 1923.
16. ———. Chlorophyllmutantem bei Gerste. Ihre Entstehung und primären Spaltungen. Hereditas 5: 49-83. 1924.
17. ———. Koppelungen und synthetische Lethalität bei den Chlorophyllfactoren der Gerste. Hereditas 8: 229-254. 1926.
18. HARLAN, H. V. Some distinctions in our cultivated barleys with reference to their use in plant breeding. U. S. Dept. Agric. Bull. 137. 1914.
19. ——— and HAYES, H. K. Occurrence of the fixed intermediate. *Hordeum intermedium Haxtoni*, in crosses between *H. vulgare pallidum* and *H. distichon palmella*. Jour. Agric. Res. 19: 575-592. 1920.
20. HAYES, H. K. and GARBER, R. J. Breeding Crop Plants. 2 edit. 438 pp. New York. McGraw-Hill Book Co. 1927.
21. HOR, K. S. Interrelation of genetic factors in barley. Genetics 9: 151-180. 1924.
22. KAJANUS, B. and BERG, S. O. Kreuzsstudien an Gerste. Hereditas 5: 287-296. 1924.
23. KEZER, A. and BOYACK B. Mendelian inheritance in wheat and barley. Colo. Agr. Exp. Sta. Bull. 249. 1918.
24. KUCKUCK, H. VON. Xenienbildung bei Gerste. Der Zuchter. 1:1:14-16. 1929.
25. MACKIE, W. W. Inheritance of resistance to rusty blotch in barley. Jour. Agric. Res. 36: 965-975. 1928.

26. MIYAKE, K. and IMAI, Y. Genetic studies in barley. *Bot. Mag. Tokyo.* 36: 25-38. 1922.
27. NEATBY, K. W. Inheritance of quantitative and other characters in a barley cross. *Sci. Agric.* 7: 77-84. 1926.
28. ————. An analysis of the inheritance of quantitative characters and linkage in barley. *Sci. Agric.* 9: 701-718. 1929.
29. NILSSON-EHLE, H. Über freie Kombination und Koppelung verschiedener Chlorophyllerheiten bei Gerste. *Hereditas* 3: 191-199. 1922.
30. OWEN, F. V. Calculating linkage intensities by product moment correlation. *Genetics* 13: 80-110. 1928.
31. ROBERTSON, D. W. Linkage studies in barley. *Genetics* 14: 1-36. 1929.
32. SIGFUSSEN, S. J. Correlated inheritance of glume colour, barbing of awns and length of rachilla hairs in barley. *Sci. Agric.* 9: 662-674. 1929.
33. TEDIN, H. and TEDIN, O. Contributions to the genetics of barley. 1. Type of spike, nakedness and height of plant. *Hereditas* 7: 151-160. 1926.
34. ————. II. The development of the kernel basis and its relation to density. *Hereditas* 9: 303-312. 1929.
35. THATCHER, R. W. Dominant and recessive characters in barley and oat hybrids. *Proc. Soc. Prom. Agr. Sci.* 33: 37-50. 1912.
36. TSCHERMAK, E. VON. Über Zuchtung neuer Getreiderassen mittelst künstlicher Kreuzung. *Zts. Landw. Versuchsw. Oesterr.* pp. 1029-1050. 1901.
37. UBISCH, G. VON. Beitrag zu einer Faktorenanalyse von Gerste. *Zts. Indukt. Abstamm. u. Vererb.* 17: 120-152.; 20: 65-117; 25: 199-220. 1917, 1919, 1921.
38. WIGGANS, R. G. A classification of the cultivated varieties of barley. N.Y. (Cornell) *Agr. Exp. Stat. Mem.* 46. 1921.

DINER DES AGRONOMES A QUEBEC

Le 14 janvier, la section québécoise de la C.S.T.A. donnait en l'honneur du Ministre de l'Agriculture, l'Hon. J. L. Perron, un magnifique dîner-causerie.

M. Adélard Godbout, M.P.P., professeur à l'école d'Agriculture de Ste-Anne, fut le conférencier de la soirée.

Le congrès des agronomes assurait à cette fête la présence de représentants de tous les comtés agricoles de la province de Québec.

A la table d'honneur, présidée par M. Léo Brown, président de la section de Québec, L'Hon. Premier Ministre, M. Taschereau, et tous ses collègues du cabinet rehaussaient cette fête agronomique.

M. Léo Brown, qui fut l'âme de toute l'organisation, en souhaitant la bienvenue à tous les convives, appuya sur la nécessité des connaissances techniques en agriculture. "Il fut un temps" dit-il, "où un finissant de nos collèges classiques aurait cru déroger à sa carrière s'il avait embrassé la profession de cultivateur. Il n'en est plus ainsi heureusement, et chaque année voit de nos bacheliers ès arts se diriger vers nos écoles d'agriculture".

Puis, présentant en termes chaleureux le conférencier, M. Adélard Godbout, il lui laissa la parole.

"La nécessité de la science agricole" fut la thèse développée par notre distingué conférencier. M. Godbout, avec les connaissances, le tact et le talent que nous lui connaissons, fit ressortir, avec chiffres à l'appui, le résultat du travail des techniciens sur les fermes de démonstration. Il exposa les besoins de l'enseignement agricole dans notre province. Il insista sur le mode de production à un minimum de prix de revient, et sur les services que nous sommes appelés à rendre à la classe agricole, dans la direction et le choix de leurs productions.

M. Godbout félicita le Ministre de l'Agriculture des succès obtenus et ajouta que les agriculteurs ont une richesse incomparable: la sympathie des dirigeants de la société et de toutes les classes. Il termina en ajoutant qu'une bonne éducation primaire est nécessaire au cultivateur s'il veut acquérir ensuite la science agricole, absolument indispensable dans l'exploitation rationnelle d'une ferme. Il fut vivement applaudi.

L'Hon. M. Perron, après avoir été l'objet d'une belle ovation, remercia M. Godbout de sa causerie, salua la présence du Premier Ministre, puis se dit heureux du fait que l'Hon. Secrétaire Provincial ait entendu la causerie du député de l'Islet. "Je suis assuré," dit-il, "que d'ici trois ans, grâce au gouvernement, nos élèves ne seront pas obligés d'aller chercher l'instruction agricole à l'étranger. Le gouvernement va dépenser, d'ici un an, la somme de \$500,000. pour donner aux écoles d'agriculture ce qu'il leur faut." Le ministre ajouta que les enquêtes agricoles ont été commencées et qu'elles se poursuivent sous la direction d'un de nos meilleurs économistes, M. Henri-C. Bois.

L'Hon. Premier Ministre prit la parole, et dit qu'il voudrait voir tout le Canada présent à ce banquet, pour qu'il se rende bien compte de ce que sont nos agronomes et notre classe agricole. En s'adressant aux agronomes, M. Taschereau ajouta qu'ils avaient la mission la plus belle et la plus patriotique. "Gagnez bien la confiance par votre conduite, efforcez-vous d'être des apôtres, des missionnaires, éclairez les jeunes dans l'école primaire, dites-leur qu'ils doivent s'attacher à la terre."

M. Sauvé, représentant le chef de l'Opposition, en quelques paroles remplies de conviction, réaffirma l'assurance de son dévouement à la classe agricole.

M. Georges Bouchard, M.P., vice-président de la Société Canadienne des Techniciens Agricoles, exposa en quelques mots les vues de notre association professionnelle.

M. de St-Victor, représentant de la République Française à Québec, ménagea pour la clôture du banquet une agréable surprise, en remettant à M. J-H. Lavoie, chef du service de l'horticulture, la décoration de Chevalier du Mérite Agricole de France.

Le plaisant devoir de remercier les conférenciers et les hôtes revint à M. R. Rousseau, doyen des agronomes.

L'hymne national "O Canada", chanté par les deux cents convives, termina ces agapes inoubliables.

Nazaire Parent.

"CORRECTION"

Dans notre article publié dans l'édition de novembre 1929, il s'est glissé trois malheureuses erreurs que nous demandons au lecteur de vouloir bien corriger.

En étudiant le facteur "pesanteur au boisseau vs pourcentage d'écale," nous disions que Love avait trouvé les deux coefficients suivants :

$$r = .237 \pm .058.$$

$$r = .188 \pm .055$$

Or ces deux coefficients devraient être précédés du signe—(négatif)

$$r = - .237 \pm .058$$

$$r = - .188 \pm .055$$

C'est ce qu'on aura compris par la suite sans doute.

Un peu plus loin, nous disions que nous avions trouvé comme coefficient de corrélation au collègue Macdonald :

$$r = .3504 \pm .045$$

La même remarque s'applique ici et notre coefficient devait être précédé du signe—(négatif).

$$r = -.3504 \pm .045.$$

Robert Raynauld.

CONCERNING THE C.S.T.A.

NOTES AND NEWS

G. P. McRostie (Toronto '12), who has been Dominion Agrostologist for the past eight years, has been appointed Professor of Field Husbandry at the Manitoba Agricultural College to succeed T. J. Harrison (Manitoba '11) who is now Assistant Commissioner on the Dominion Board of Grain Commissioners.

L. C. McOuat (McGill '15) has resigned his position as Bacon Specialist with the Dominion Live Stock Branch to accept an appointment with the Canadian Pacific Railway Company as General Agricultural Agent for Eastern Canada, with headquarters at Montreal, P.Q. Mr. McOuat took up his new duties on February 15th.

G. R. Paterson (Toronto '24) has been appointed Agricultural Fieldman with the American Cyanamid Company. Mr. Paterson commenced his new duties on February 1st and his headquarters are at Guelph, Ont.

A. Leahey (Alberta '25) is taking graduate work in the Department of Geology, University of Wisconsin, Madison, Wis.

H. J. Siemens (Manitoba '25), who has been County Agent under the North Dakota Department of Agriculture for the past two years, has accepted an appointment as Farm Supervisor for the Canada Colonization Association, 460 Main Street, Winnipeg, Man.

J. A. Martin (Montreal, '28) is taking graduate work at Cornell University. His mailing address is 210 College Ave., Ithaca, N.Y.

J.W. Howe (Alberta, '25) has changed his address to c/o W. W. Howe, 10012-101A Avenue, Edmonton, Alta.

C. J. Watson (McGill, '21), Assistant Chemist at the Central Experimental Farm since 1921, has been appointed Chemist.

W. Edward Lindsay (McGill, '29) is taking a year's graduate work in entomology at the University of Minnesota.

Auguste Scott (Montreal, '24) is with the Quebec Department of Agriculture, specializing in soils and fertilizers. His mailing address is Rural Economics Branch, Parliament Buildings, Quebec.

J. M. A. St. Denis (Montreal, '26), Inspector of Demonstration Farms under the Quebec Department of Agriculture, has been transferred to Sorel. His mailing address is P. O. Box 101, Sorel, P.Q.

J. F. Andrew (Toronto, '23), formerly Farm Manager and Lecturer in Animal Husbandry at the Vermilion School of Agriculture, has been appointed Assistant Deputy Minister of Agriculture for Alberta.

A. E. Davey (Toronto, '25) is taking graduate work in the Department of Plant Pathology, University of California, Berkeley, Cal.

APPLICATIONS FOR MEMBERSHIP

The following applications for regular membership have been received since February 1, 1930.

Gerrie, H. (Saskatchewan, 1928, B.S.A.), Saskatoon, Sask.

Murray, R. P. (Toronto, 1920, B.S.A.), Penticton, B.C.

McKenzie, Duncan (British Columbia, 1929, B.S.A.), Vancouver, B.C.

Putnam, D. F. (Toronto, 1927, B.S.A.), Macdonald College, P.Q.

Spilsbury, R. H. (British Columbia, 1929, B.S.A.), Victoria, B.C.

Webster, J. L. (Toronto, 1925, B.S.A.), Penticton, B.C.

Wildman, E.C. (Toronto, 1922, B.S.A.), Toronto.

ACTING GENERAL SECRETARY

Mr. L. H. Newman, Honorary Secretary of the C.S.T.A. since its organization, is Acting General Secretary and Managing Editor of *Scientific Agriculture* until a successor to Mr. Grindley is appointed.

VACANCIES IN DOMINION DEPARTMENT OF AGRICULTURE

The Civil Service Commission at Ottawa is advertising the following vacancies in the Dominion Department of Agriculture. Applications should be addressed to the Secretary of the Commission:

Senior Seed Analyst. Initial salary \$1,620 per annum up to a maximum of \$1,980 per annum. To be located at Winnipeg, Man. Applications must be filed not later than March 13, 1930.

Cereal Chemist. Initial salary \$2,820 per annum up to maximum of \$3,300 per annum. To be located at Ottawa. Applications must be filed not later than April 17, 1930.

Junior Cereal list. (Temporary). Initial salary \$1,620 per annum up to a maximum of \$1,920. To be located in Manitoba. Applications must be filed not later than March 15, 1930.